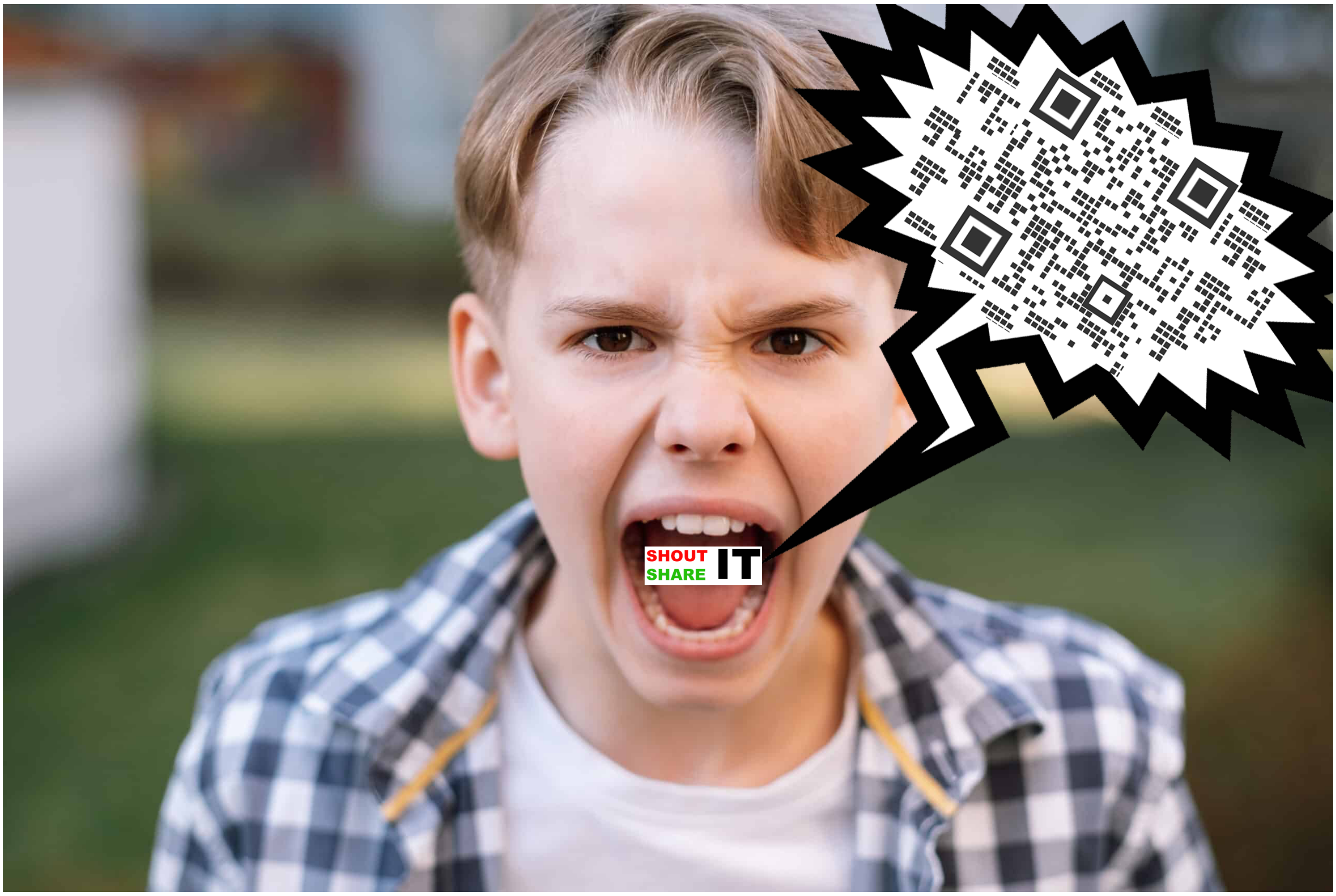
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NUMBERS 410–436

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THE COLOR PATTERN OF *Sonora michoacanensis* (Dugès) (SERPENTES, COLUBRIDAE) AND ITS BEARING ON THE ORIGIN OF THE SPECIES

Arthur C. Echternacht

Abstract. The extensive variation in color pattern of the 31 known specimens of *Sonora michoacanensis* is described and a model illustrating the relationships of the major components presented. *Sonora aequalis* Smith and Taylor is placed in the synonymy of *Sonora michoacanensis mutabilis* Stickel from which it differs only slightly in color pattern. It is suggested that *S. michoacanensis* evolved from a bicolor, banded ancestor within the *S. semiannulata* group or from a common ancestor at the southern edge of the Mexican Plateau following habitat shifts associated with climatic changes during the Pleistocene. *Sonora michoacanensis* is interpreted as an imperfect Batesian mimic of elapid coral snakes (*Micrurus* sp.), intermediate in an evolutionary sequence beginning with the bicolor, banded ancestor and leading toward a more perfect, tricolor mimic. Known locality records of *S. michoacanensis* are mapped and selected meristic data presented in tabular form.

Introduction

The genus *Sonora* (Serpentes, Colubridae) is represented in México, at the southern limit of its range, by *Sonora michoacanensis* (Fig. 1). *Sonora m. michoacanensis* (Dugès) is found in arid to semiarid habitats from the upper Balsas Basin in Puebla to the lower slopes of the Sierra de Coalcomán and southeastern Colima, whereas *S. m. mutabilis* Stickel occupies foothills of the Sierra Madre Occidental from southern Jalisco to Nayarit and Zacatecas (Duellman, 1961; Zweifel, 1956). The principal diagnostic difference between the subspecies is that *S. m. michoacanensis* has an unmarked tail, whereas the tail of *S. m. mutabilis* is banded. The two subspecies will be considered together in the discussion of color pattern to follow.

The last review of this assemblage was by Stickel (1943).

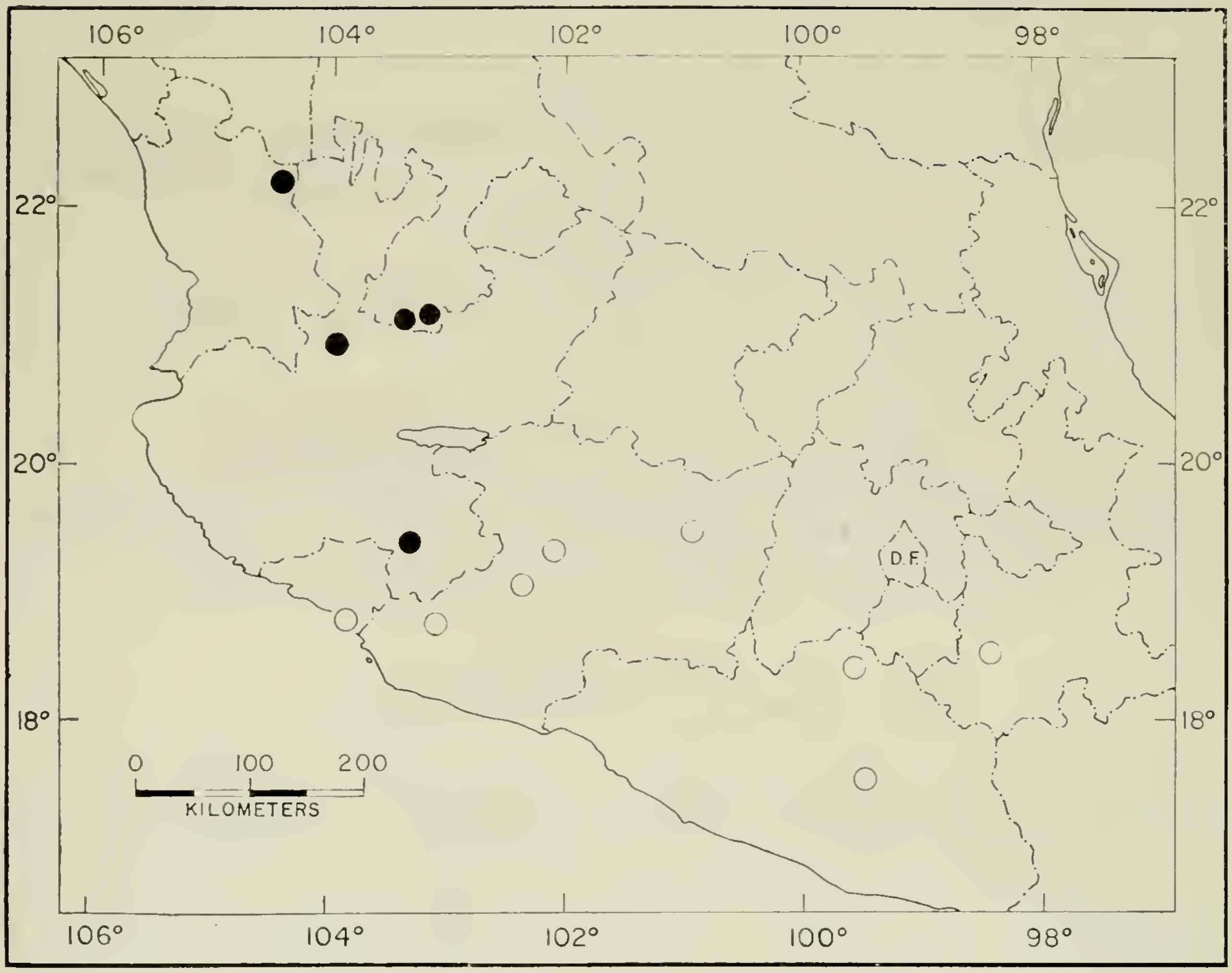

Figure 1. Localities of documented specimens of *Sonora michoacanensis* in México. Hollow circles: *S. m. michoacanensis;* solid circles: *S. m. mutabilis.* D. F. is the Distrito Federal.

His clear and concise discussion included a detailed description of a single unusual specimen which Smith and Taylor (1945) subsequently named, with no further description, *Sonora aequalis.* Stickel had been unwilling to base a new species on the single specimen because it was of unknown provenance and because it differed from *S. m. mutabilis* only in color pattern, a character known to be highly variable in *S. michoacanensis.* Stickel presented data on all 18 specimens of *S. michoacanensis* (including *S. aequalis*) then known but was able to examine only 11 of these. The holotype of *S. m. michoacanensis* was lost, and he designated a neotype (Fig. 2), and described *S. m. mutabilis.* The recent discovery of a specimen intermediate in color pattern to "typical" *S. m. michoacanensis* and *S. aequalis* and the availability of 14 specimens of *S. michoacanensis* collected over the 30 years since Stickel's paper have made possible a re-examination of the variation in color pattern of the species and a reassessment of the taxonomic status of *S. aequalis.* Al-

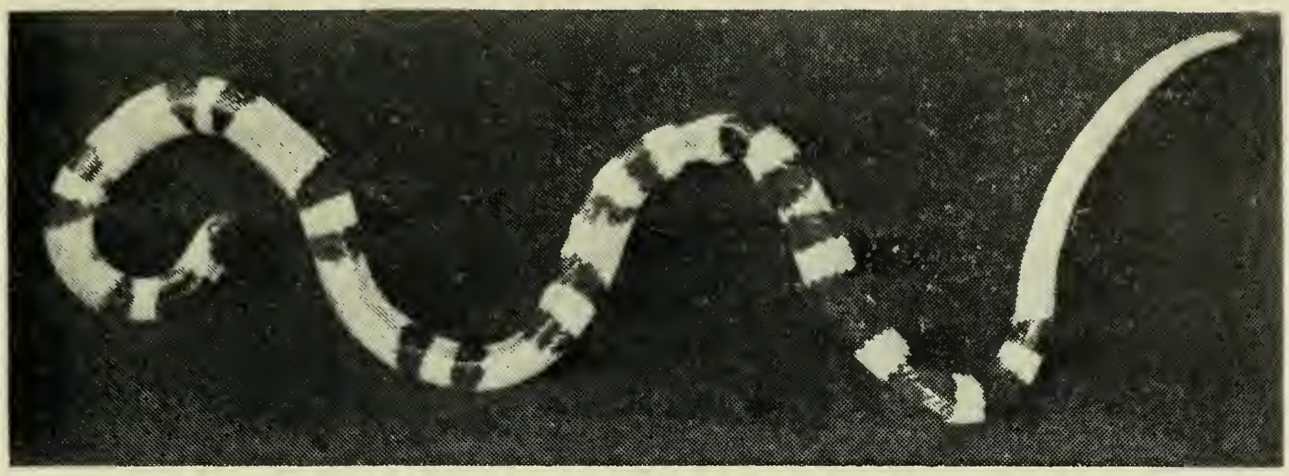

Figure 2. Neotype of *Sonora michoacanensis michoacanensis,* BMNH 1946. 1.14.65.

though this paper emphasizes color pattern, I have summarized meristic data for all known specimens (Tables 1 and 2) so that these data will be available to others. Counts of ventral scales were made according to the method of Dowling (1951) and do not include the anal scale. Counts of subcaudal scales exclude the tip. For these reasons, data given here may differ slightly from those presented by Stickel (1943: 114–115). Where means are given for scale counts they are based only upon specimens that I was able to examine myself. The color descriptions are based on preserved specimens unless stated otherwise.

Acknowledgements. William E. Duellman, Richard D. Estes, Ernest E. Williams and Richard G. Zweifel have all read the manuscript in its formative stages and I am grateful for their thoughtful criticism. The research was funded in part by a grant from the Boston University Graduate School (GRS BI-15-BIO). I am indebted to the following individuals and institutions for the loan of specimens: William E. Duellman (University of Kansas Museum of Natural History, KU), Herbert S. Harris (Personal Collection, RS-HSH), Hymen Marx (Field Museum of Natural History, FMNH), Hobart M. Smith and Dorothy Smith (University of Illinois Museum of Natural History, UIMNH), David B. Wake (Museum of Vertebrate Zoology, MVZ), Charles F. Walker and Scott M. Moody (University of Michigan Museum of Zoology, UMMZ), Ernest E. Williams (Museum of Comparative Zoology, MCZ) and Richard G. Zweifel (American Museum of Natural History, AMNH). Herbert S. Harris kindly provided a color slide of a living snake, and A. F. Stimson was instrumental in obtaining data

on, and photographs of, the three specimens in the British Museum of Natural History (BMNH). Photographs of other specimens were prepared by Frederick W. Maynard.

VARIATION OF COLOR PATTERN

It is almost impossible to exaggerate the extent of variation in color pattern exhibited by the series of *Sonora michoacanensis* presently available for study. Only the pattern of the head and neck seem relatively invariant. There is always a dark "mask" on an otherwise pale head. The mask may include the rostral and internasal scales, but typically begins between the rostral and a line connecting the anterior margins of the orbits. This dark area surrounds the eye and may extend forward on the side of the head to include all or parts of the nasal, loreal, preocular, anterior supralabials and those in contact with the orbit, the postorbitals and the temporals. Dorsally it covers the frontal, supraoculars and (often) parts of the prefrontals, terminating with a crescentic posterior margin on the parietals. There is a black or dark brown nuchal band (collar) separated from the mask by a light-colored band. The nuchal band may completely encircle the body or may be interrupted midventrally. The anterior margin of the nuchal band is variable in shape but the posterior margin is usually straight across. The nuchal band is followed posteriorly by a light-colored band, usually three to five scales wide, which is, in turn, followed by another dark band. The last is a "half-saddle," its anterior margin straight across and its posterior margin crescentic. The half-saddle may completely encircle the body or be interrupted at the midline below.

One specimen (FMNH 37141, Fig. 3A) has no pattern whatsoever except that just described. All others have some dorsal banding pattern. This overall dorsal pattern ranges from one of only saddle-shaped triads consisting of a median gray band abutted fore and aft by black (*e.g.*, AMNH 74951, Fig. 4B) to one of only broad black bands separated by a narrower gray band corresponding to the median gray band of the triads (*e.g.*, KU 106286, Fig. 4C–4D). Individual snakes may have combinations of triads and broad black bands (Fig. 3B, 3E–3F). Occasionally, the broad black bands are partially split by light pigment extending up from the venter (*e.g.*, MVZ 76714, Fig. 3B). The light pigment (= ground color) may be off-white, gray, salmon or flesh-colored but to comply with Stickel's

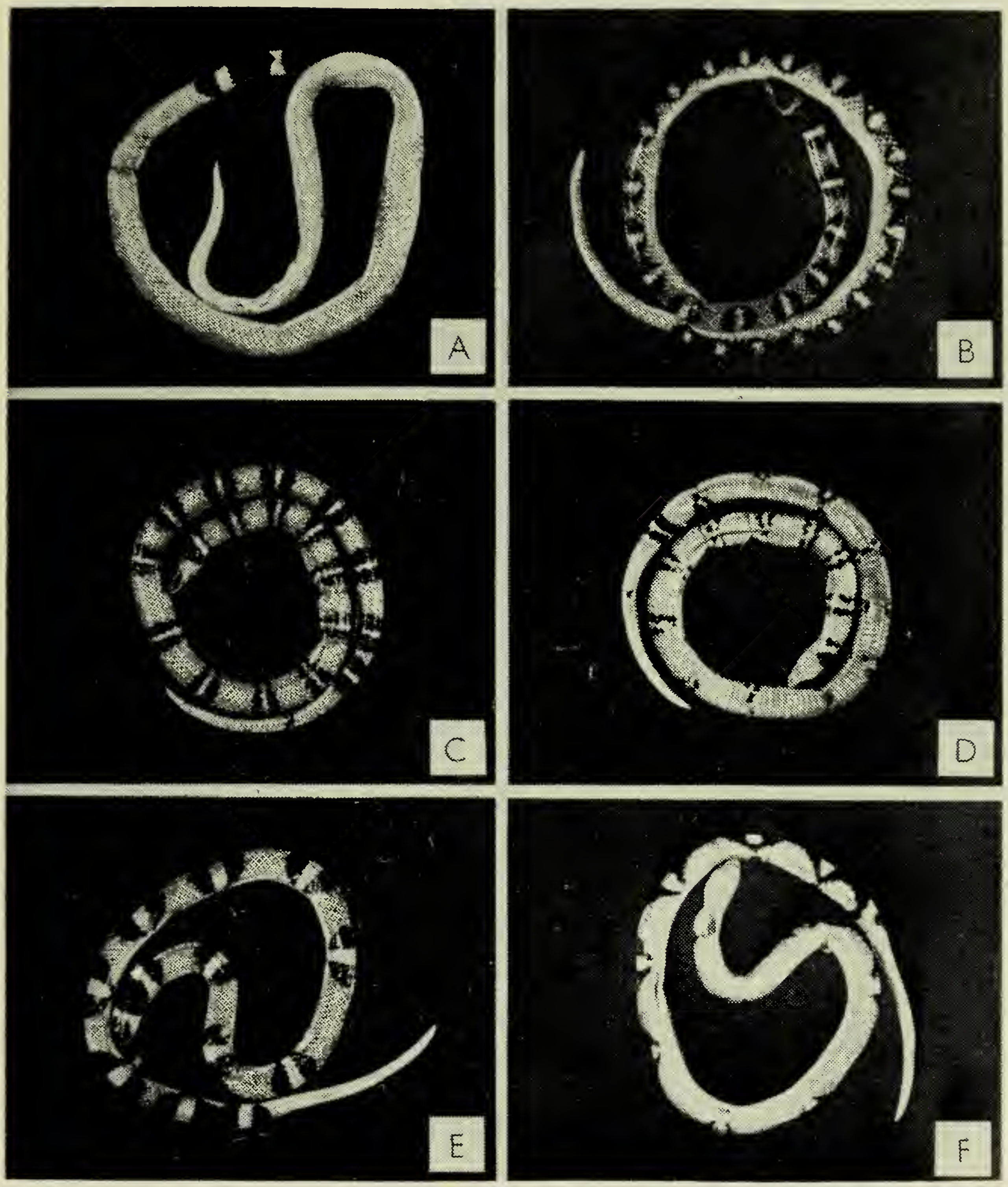

Figure 3. *Sonora michoacanensis michoacanensis:* A. FMNH 37141, dorsal; B. MVZ 76714, dorsal; C. UMMZ 109904, dorsal; D. UMMZ 109904, ventral; E. FMNH 39129, dorsal; F. FMNH 39129, ventral.

(1943) terminology it is referred to as red herein. The black bands may not reach the ventral scutes but if they do, they may or may not extend across them to form rings. The same is true for the black elements of the triads which may not reach the ventral scutes, may completely ring the body in such a way that the median gray band is also a ring, or may be joined along the midventral line so that the median gray band is incomplete. All three possibilities are seen on UMMZ 109904 (Fig. 3D). If a snake has both triads and broad black bands, it is usual for the triads to be found anteriorly and the black bands posteriorly (*e.g.,* FMNH 39129, Fig. 3E).

Taylor (1937) provides a description of color-in-life of *Sonora michoacanensis michoacanensis* from Guerrero and Jalisco. The ground color is red or pinkish, the dark elements of the triads black and the middle element of the triads yellow or gray-cream. A single specimen from Colima is similarly colored (Harris and Simmons, 1970), but Duellman (1961) described the middle element of the triads as white in a series of specimens from Michoacan.

A specimen of *Sonora michoacanensis michoacanensis* collected in Jalisco by Percy Clifton (KU 106286, Fig. 4C–4D) is unusual in that none of the black bands is split by red and there are no triads. None of the black bands except the nuchal and that immediately posterior to it reaches the ventral scutes. The broad black bands are expanded laterally just above the ventral scutes and some contact adjacent, similarly expanded bands. The black and gray bands (black and pale salmon in this specimen) are subequal in width. This pattern is approached in MVZ 76714 (Fig. 3B) but, prior to the discovery of KU 106286, no *S. michoacanensis* were known with a pattern entirely of unsplit black bands alternating with gray bands of approximately equal width. In this respect, KU 106286 resembles *Sonora aequalis* (MCZ 6444, Fig. 4E–4F).

In addition to presence or absence of caudal banding, *Sonora michoacanensis michoacanensis* and *S. m. mutabilis* differ in the number of gray bands of females, the number of complete triads of males, and the number of black bands unsplit by red of males and females. Sexual differences are evident for all three of these characters in *S. m. mutabilis,* but not in *S. m. michoacanensis* (Tables 1 and 2). In addition, there is a statistically significant ($t = 3.91$, $P < .01$ with 23 degrees of freedom) difference between the subspecies in total (left plus right) number of infralabials: The mean and standard devia-

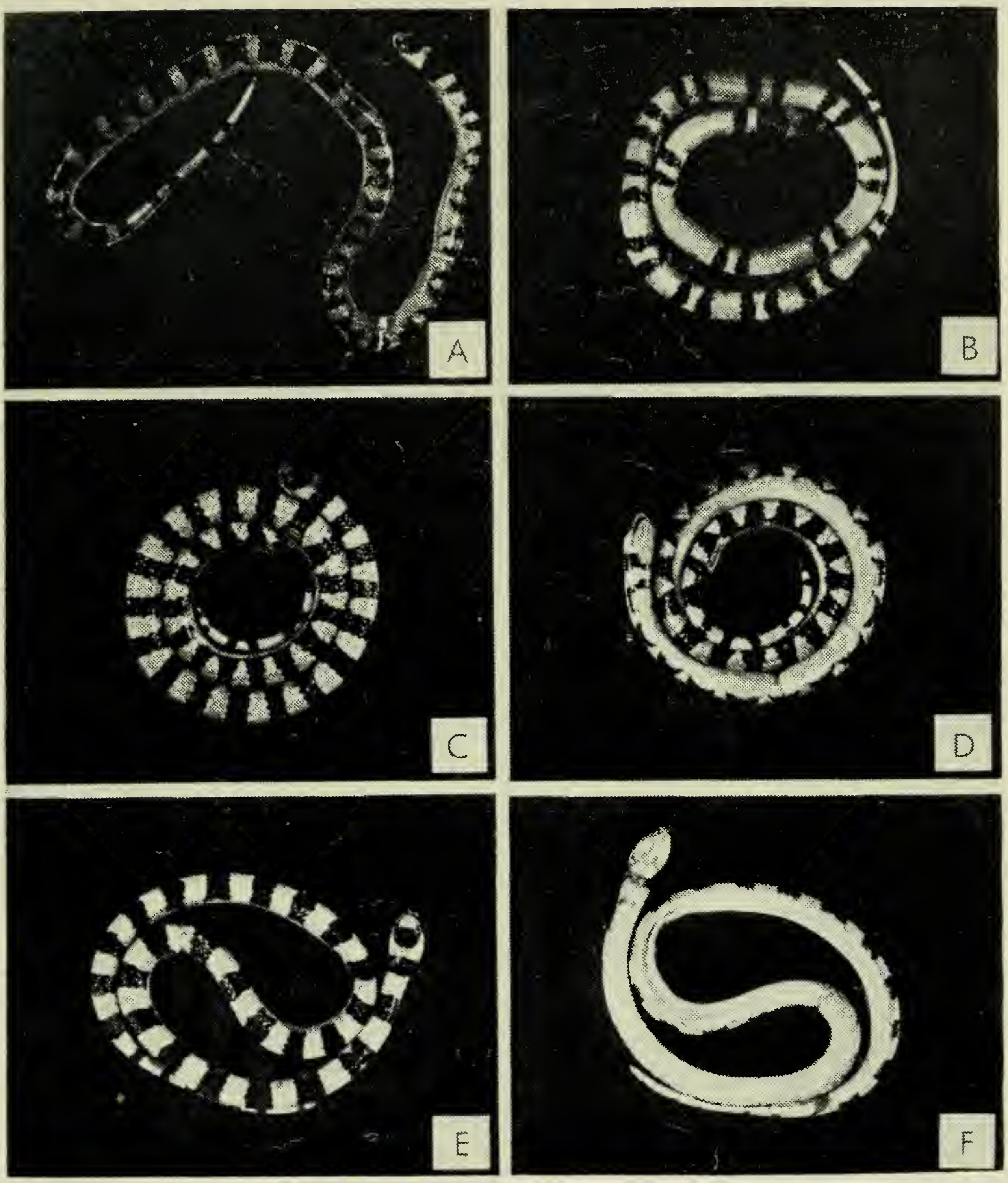

Figure 4. *Sonora michoacanensis mutabilis:* A. UIMNH 18754, dorsal; B. AMNH 74951, dorsal; C. KU 106286, dorsal; D. KU 106286, ventral; E. MCZ 6444, dorsal; F. MCZ 6444, ventral. MCZ 6444 is the holotype of *Sonora aequalis.*

tions for *S. m. michoacanensis* are 13.5 ± 1.09, for *S. m. mutabilis* 12.1 ± 0.30. The number of infralabials is not sexually dimorphic for either subspecies. It is notable that of the seven *S. m. michoacanensis* with 13 fewer infralabials, three are from near Coalcomán, Michoacan (UMMZ 106604–6), where a single specimen (UMMZ 109904, Fig. 3C–3D) has one irregularly shaped caudal band, possibly indicative of intergradation. Three other specimens with fewer than 14 infralabials (KU 23791, MCZ 33650) or indications of low numbers of infralabials (MVZ 45123) are from near Chilpancingo, Guerrero. The seventh such specimen is the missing holotype from "Michoacan" [Cope, 1884(1885)].

The Taxonomic Status of *Sonora aequalis*

The only known specimen of *Sonora aequalis* (MCZ 6444)[1] is recorded as being from Matagalpa, Nicaragua, but Stickel (1943: 117) concluded that Matagalpa was most likely only the shipping point for material collected by W. B. Richardson. Other specimens in the same bottle as the snake and the locality label were two *Eumeces lynxe lynxe* (*fide* Joseph R. Bailey *in* Stickel, 1943: 118), a lizard whose range overlaps that of *Sonora michoacanensis mutabilis.* This and other evidence led Stickel to conclude that MCZ 6444 was found within or near the range of *S. m. mutabilis.* The pattern of MCZ 6444 consists of 26 black bands and 25 gray bands, the bands being all of approximately the same width (the basis for the name *aequalis*). None of the black bands is split by red but several are ventrally concave (Fig. 4F). The nuchal band completely rings the body, but details in this region are obscure because of damage to the specimen. None of the black bands on the body reaches the venter and none is expanded laterally as in KU 106286. The cephalic pattern is the same as that of *S. michoacanensis* and the tail is banded in triads as is characteristic of *S. m. mutabilis.* The specimen is badly faded and no colors other than black and gray are apparent.

In view of the great variation in dorsal body pattern evident within the subspecies of *Sonora michoacanensis,* it does not seem to me that the differences between *S. aequalis* and *S. m.*

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[1] Stickel (1943: 117), in error, recorded the snake as an uncatalogued specimen in the University of Michigan Museum of Zoology. How and why it got to Michigan and thence back to the Museum of Comparative Zoology remains a mystery.

mutabilis are great enough to warrant taxonomic recognition of *S. aequalis.* These differences are certainly no more startling than those of the almost patternless FMNH 37141 (Fig. 3A). KU 106286 (Fig. 4C–4D) seems to be a logical intermediate in pattern between *S. m. mutabilis* and *S. aequalis.* Extensive collecting in México and Nicaragua over the last 30 years has brought to light no additional specimens of *S. aequalis,* but a number of additional specimens of "typical" (if that word is admissable) *S. michoacanensis* have been collected in México. Of course, no additional specimens similar to FMNH 37141 have been found either.

It may be questioned whether it is any more justifiable to "sink" a species on the basis of one specimen (KU 106286) than it was to name one in the first place (*S. aequalis,* MCZ 6444). But the discovery of KU 106286 has provided an important link in what appears to be a continuum in pattern variation extending from the pattern (or, rather, lack of pattern) exhibited by FMNH 37141 to that of MCZ 6444 with the presence or absence of caudal banding superimposed. The possibility that KU 106286 is a hybrid of *S. aequalis* and *S. m. mutabilis* cannot be ruled out, but its likelihood is reduced by the absence of additional specimens of *S. aequalis* in collections made over the past 30 years.

Relationships of the Components of Color Pattern and the Origin of *Sonora michoacanensis*

Figure 5 illustrates my concept of the relationships of the various components of dorsal color pattern of *Sonora michoacanensis.* Certainly no ontogenetic sequence is implied, but the initial stages (Fig. 5A–5B) may be interpreted to suggest something of the origin of the species. The ancestor of *S. michoacanensis* may have been patterned very much like MCZ 6444. Progressive erosion of the broad black bands (Figs. 5B–5D) would yield triads (Fig. 5E). A complex genetic mechanism would allow individual snakes to have various combinations of triads and unsplit black bands or triads in varying numbers and of varying distances apart. With the exception of the virtually patternless FMNH 37141, the most consistent element of color pattern is the gray band between adjacent unsplit black bands or as the median element in a triad (Stickel, 1943: 116).

The banding pattern of MCZ 6444 is very similar to that of the banded forms belonging to the *Sonora semiannulata* group

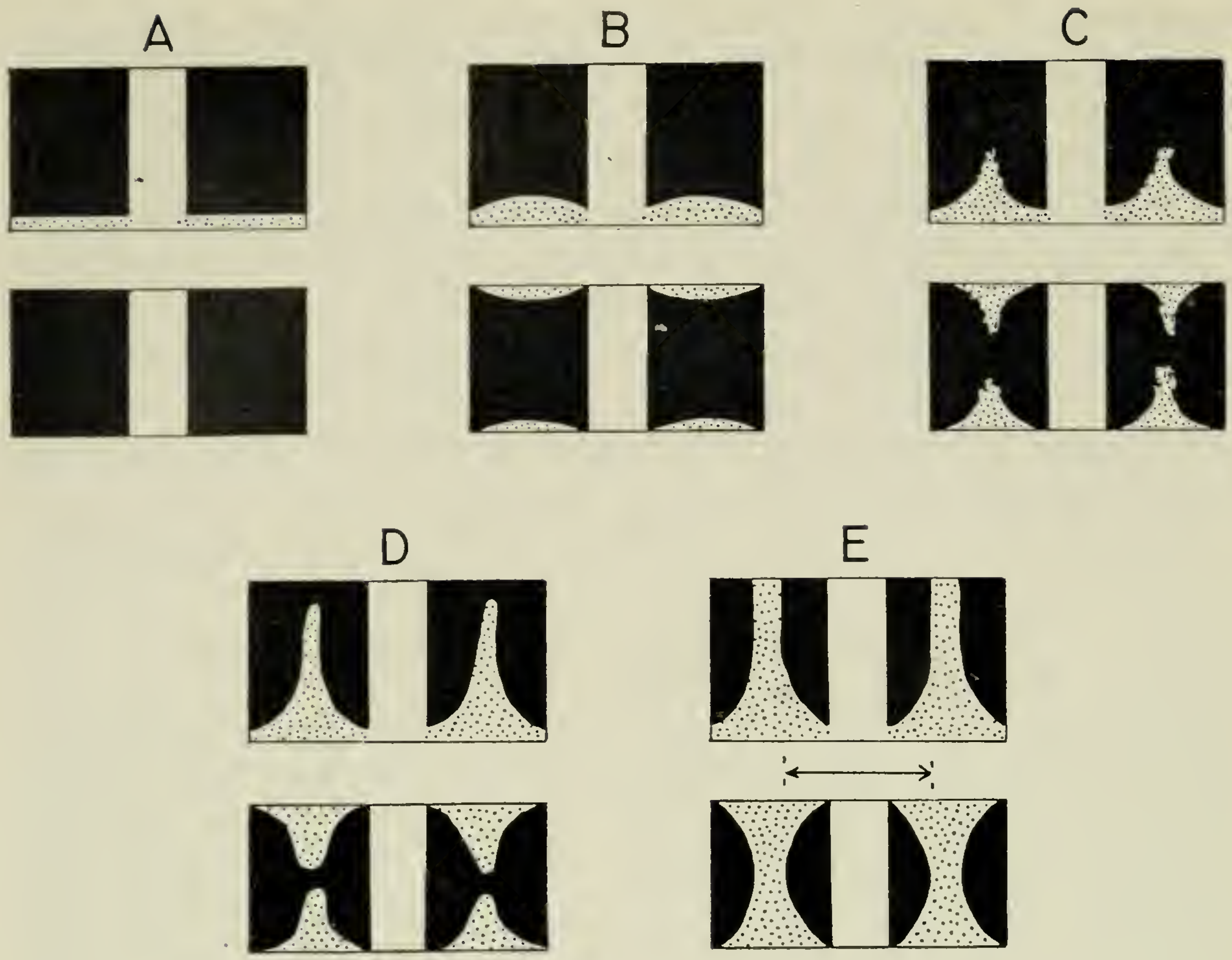

Figure 5. Diagrammatic representation of color pattern variation of *Sonora michoacanensis*. The arrow spans one complete triad. Black = black, white = white or yellow, stippled = red. Upper figure of each pair, lateral view; lower figure, dorsal view.

of southwestern United States and northern México (Stickel, 1938: 184–186; Stebbins, 1966). MCZ 6444 and all *Sonora michoacanensis* have 15 dorsal scale rows with no reduction as do some members of the *S. semiannulata* group. *Sonora michoacanensis* is distinguishable from members of the *S. semiannulata* group in morphology of the hemipenis (Stickel, 1943: 112), but the two groups are very similar in scutellation, teeth, dentigerous bone structure, microscopic scale striation and, generally, color pattern (Stickel, 1943: 110). It seems reasonable to assume that, as Stickel (1943: 118) seems to have suggested, *S. michoacanensis* had its origin within the *S. semiannulata* group or that the two groups had a common ancestor.

Members of the *Sonora semiannulata* group are presently found (Stebbins, 1966) in the southern Warm Temperate and Subtropical Climatic Zones as broadly mapped by Dorf (1959: 198). These major climatic belts shifted southward with glacial advance during the Pleistocene (Dorf, 1959: 195) and the range of the *S. semiannulata* group or its ancestor may have been depressed southward into the area presently occupied by *S. michoacanensis. Sonora michoacanensis* may have differentiated as a relict at the southwestern fringe of the Mexican Plateau when climatic zones retreated northward with retraction of Wisconsin glaciation.

THE SELECTIVE SIGNIFICANCE OF THE COLOR PATTERN OF *Sonora michoacanensis*

A number of New World colubrid snakes have tricolor banding patterns which are reminiscent of the red, black and yellow or white patterns well known among the highly venomous coral snakes (Elapidae). Considerable circumstantial evidence has accumulated that the colubrids are mimics of those coral snakes with which they are sympatric and are thus avoided by those predators which have learned to avoid coral snakes (Dunn, 1954; Hecht and Marien, 1956; but see Brattsrom, 1955). Three kinds of mimicry in snakes have been recognized (Wickler, 1968: 118). Batesian mimicry where the model is highly venomous and the mimic nonvenomous, Müllerian mimicry where both models and mimics are highly venomous and reinforce one another, and Mertensian mimicry where the model is highly venomous and the mimic mildly venomous. *Sonora michoacanensis* is a Batesian mimic of coral snakes of the genus *Micrurus* (Hecht and Marien, 1956: 345).

The ranges of several species of *Micrurus* overlap or are contained within the range of *Sonora michoacanensis* (Roze, 1967). The basic color pattern of these elapids is one of black rings bordered on either side by narrower yellow or white rings, these triads being separated along the body by red. The order of the colors in the triads is, therefore, different from that of *S. michoacanensis.* This difference is probably of little significance insofar as mimicry is concerned, as the distinction is difficult to make, even for a trained observer, when the snakes are come upon suddenly or when they are moving. Potential predators presumably have the same difficulty and Hecht and Marien (1956: 339) present evidence that the order of the colors is less important that the presence of the bright, contrasting colors themselves. In other words, the mimic need not be an exact replica of the model to gain a selective advantage.

The concept of Batesian mimicry requires that the mimic be less abundant than the model. If relative abundance in museum collections is an accurate reflection of relative abundance in nature, this requirement is met in that *Micrurus* is much better represented. It should, however, be noted that *Sonora michoacanensis* is a secretive species and may not be as rare as collections indicate. In a few areas where collecting has been repeated or intensive, small series have been obtained (see list of specimens).

There are two alternative hypotheses concerning the origin of mimicry: 1) The mimic evolves in a single step by mutation (Goldschmidt, 1945), and 2) the mimic evolves gradually through selection of modifier genes improving upon an original mutant that had itself a slight selective advantage (Fisher, 1930; E. B. Ford, 1953). Sheppard (1959) strongly supports the second hypothesis and suggests that mimetic patterns are controlled by supergenes that have evolved stepwise. Recent experimental work by H. A. Ford (1971) supports the alternative of gradual evolution and provides evidence that bird predators avoid a new partial mimic, strongly preferring a familiar nonmimetic form of prey.

If my interpretation is correct, *Sonora michoacanensis* evolved from a bicolor, banded ancestor belonging to the *S. semiannulata* group. Although bicolor members of this group are sympatric with a coral snake (*Micruroides euryxanthus*) over much of their range, relative numbers of specimens in museums suggests the colubrid to be much the commoner snake. Thus, Batesian mimicry could not develop. To the south, however, the Pleistocene relict population ancestral to *S. michoacanensis* may have been small relative to the populations of *Micrurus* with which they evolved. If this was indeed the case, *S. michoacanensis* may as yet have not been perfected as a mimic and should be considered as intermediate in an evolutionary sequence leading from a nonmimetic, bicolor, banded ancestor toward a snake with a pattern of only triads. As there seems to be no geographic trend in color pattern except the presence or absence of caudal bands and the generally better mimetic pattern of male *S. m. mutabilis* (see below), the gradual perfection of mimicry seems to be proceeding over the entire range of *S. michoacanensis*. The extreme variability in color pattern evident in the present population would result from lack of fixation at each of the major and minor gene loci responsible for pattern. This diversity of pattern would be tolerated because all of the intermediate types are to some degree mimetic except those that have bicolor banding patterns (*e.g.*, MCZ 6444 and KU 106286) or are nearly patternless (*e.g.*, FMNH 37141). Such extremes are expected at low frequencies where inheritance is polygenic and where fixation has not occurred (Strickberger, 1968). The pattern of *S. michoacanensis* may be regarded as both protective in a mimetic sense and as concealing or disruptive (Brattstrom, 1955). Hecht and Marien (1956: 346) have suggested that, "Banding may be an intermediate step through which a disruptive pattern is converted to a ringed, warning pattern, but functioning in both ways." It seems equally likely that the disruptive stage is intermediate to banded and tricolor, warning patterns.

An interesting and unexplained observation is that male *Sonora michoacanensis mutabilis* are, by virtue of having more complete triads (Table 2), better mimics than females and than both sexes of *S. m. michoacanensis*. Among butterflies, mimetic patterns are often sex-limited to females, as are other, nonmimetic, polymorphisms (Sheppard, 1959: 137). E. B. Ford (1953) has attributed this phenomenon to the importance of visual stimuli in the courtship of butterflies. Females make a choice of mates largely on the basis of visual cues and Ford (1953: 68) reasons that a new color pattern in males might not stimulate a female to copulate. In moths, where olfactory courtship stimuli largely replace visual cues, both sexes may be polymorphic (Sheppard, 1959: 137). Noble (1937) reviewed the role of sense organs in the courtship of snakes and concluded that chemical and tactile senses play the primary roles in sex discrimination and courtship, respectively. Vision was found to be important only in that movement attracts snakes during the breeding season. Nothing at all is known of the behavior of *S. michoacanensis*, but it seems unlikely that the sexual dichromatism of *S. m. mutabilis* serves as an aid to sex discrimination or courtship. There are no clues as to why sexual dichromatism should be pronounced only in *S. m. mutabilis* and not in *S. m. michoacanensis*.

The color pattern variation exhibited by *Sonora michoacanensis* is at least equaled by that of *Sonora aemula* Cope of southern Sonora and Chihuahua, México (Bogert and Oliver, 1945: 374; Zweifel and Norris, 1955: 244; Nickerson and Heringhi, 1966: 136). *Sonora aemula* is rare in collections (Nickerson and Heringhi knew of only ten specimens), but it, like *S. michoacanensis*, is probably locally more abundant than collections indicate. Five of the known specimens were found in or near Alamos, Sonora. The species is sympatric with both *Micruroides* and *Micrurus* and one specimen (*e.g.,* Arizona State University No. 6611; Nickerson and Heringhi, 1966, fig. 1) may have typical *Micruroides*-like triads (white-black-white), *S. michoacanensis*-like triads (black-white-black), or expanded triads (black-white-black-white-black) like some *Micrurus* from southern México and Guatemala. The area between the triads is red. Mimicry in *S. aemula* may be at the same stage of development as that which I have suggested for *S. michoacenensis,* as may mimicry in some species of the *venustissimus* and *annulatus* groups of the genus *Scaphiodontophis* in Central America (Taylor and Smith, 1943). *Scaphiodontophis* is a Batesian mimic of both *Micrurus* and the mildly colubrid *Erythrolamprus* (Hecht and Marien, 1956: 342).

KNOWN SPECIMENS OF *Sonora michoacanensis*

The holotype of *Contia michoacanensis* Dugès (Cope), 1884 (1885) (= *Sonora michoacanensis*) has been lost, and Stickel (1943: 113) designated BMNH 1946.1.14.65 as neotype. BMNH specimens have been recatalogued since Stickel's (1943) paper and both old and new catalogue numbers appear in the listing to follow. Stickel (1943: 115) examined an uncatalogued specimen of *S. m. mutabilis* in the American Museum of Natural History which was "tied with" (Stickel, 1943) AMNH 19714–19716, but the present whereabouts of this specimen is unknown (W. H. Stickel and R. G. Zweifel, personal communications). Zweifel (1956: 6) has questioned the locality data of all four specimens. They are said to have been collected in Distrito Federal, México, but this is far removed from the range of the subspecies as presently understood from well-documented specimens (Fig. 1) and they are given as "Locality Unknown" below. Stickel (1943) cited specimens in the collections of E. H. Taylor and H. M. Smith by field number. These specimens have all been deposited in museums, and both field numbers (preceded by "HMS") and museum catalogue numbers are given below.

Sonora michoacanensis michoacanensis (18). COLIMA: Between Tecomán and Boca de Apiza, RS 596 HSH. GUERRERO: Chilpancingo Region, KU 23790–1, MCZ 33650, MVZ 45123; 16 km S Taxco, UIMNH 25063 (HMS 5440, holotype of *Sonora erythrura* Taylor, 1937); locality unknown, unnumbered specimen in the Museo Alfredo Dugès, Colegio del Estado Guanajuato. MICHOACAN: Apatzingán, FMNH 39128–9; Apatzingán, Hacienda California, FMNH 37141; 3.2 km E Coalcomán, 1364 m, UMMZ 109904–6; 12.2 km S Tzitzio, 1121 m, UMMZ 119457; 16 km S Uruapan, MVZ 76714; locality unknown, BMNH 1946.1.14.65 (formerly BMNH 1903.3.21, neotype), the holotype (presumed lost). PUEBLA: 10 km SE Matamoros, UIMNH 41688.

Sonora michoacanensis mutabilis (13). JALISCO: near Magdalena, FMNH 105296 (HMS 4659, paratype), FMNH 105257 (HMS 4661, holotype), UIMNH 18754 (HMS 4660, paratype); 6.5 km S Tecalitlan, MVZ 71356. NAYARIT: Jesus Maria, AMNH 74951. ZACATECAS: 8.8 km S Mayahua, 1212 m, KU 106286; Mezquital de Oro, BMNH 1946.1. 14.63 (formerly BMNH 92.10.31.42, paratype), BMNH 1946.1.14.64 (formerly BMNH 91.10.31.43, paratype). LOCALITY UNKNOWN: AMNH 19714–6 (paratypes), specimen "tied with" AMNH 19714–6 (presumed lost), MCZ 6444 (holotype of *Sonora aequalis* Smith and Taylor).

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ADDED IN PROOF: Mr. Scott M. Moody has kindly called my attention to an additional specimen of *Sonora michoacanensis mutabilis* obtained too late for inclusion in this study. The snake (UMMZ 131666) is typical of the subspecies and was found at Presa de El Molino, El Molino in Jalisco, México.

Specimen	Sex	Body Length mm	Tail Length mm	Number of Temporals (Left/Right)	Number of Supralabials (Left/Right)	Supralabials Entering Eye (Left/Right)	Number of Infralabials (Left/Right)	Ventrals Excluding Anal	Caudals Excluding Tip	Number of Gray Bands	Number of Black Bands Not Split by Red	Number of Complete Triads	Source
Holotype	Male	160	35	1-2/1-2	7/7	3-4/3-4	6/6	152[1]	37(+?)[1]	8 or 7[1]	2	-	Cope, 1884 (1885); Stickel, 1943
BMNH 1946.1.14.65	Male	244	56	-	-	-	-	165[1]	44[1]	12	3	8	Stickel, 1943; Stimson, Personal Communication
FMNH 37141	Male	205	50	1-2/1-1	7/7	3-4/3-4	7/7	152	44	1	0	0	Present Study; Stickel, 1943
UIMNH 25063	Male	110	23	1-2/1-1	8/8	3-4/3-4	7/7	163	46	15	7	6	Present Study; Stickel, 1943
KU 23790	Male	237	46	1-2/1-2	7/7	3-4/3-4	7/7	177	41	16	11	3	Present Study
KU 23791	Male	275	55	1-1/1-1	7/6	3-4/2-3	7/6	175	42	15	5	8	Present Study
UMMZ 119457	Male	211	47	1-2/1-2	7/7	3-4/3-4	7/7	157	41	11	4	4	Present Study
Mean		206	44.6					164.8	42.8	11.7	4.6	4.8	
Standard Deviation		55.6	11.8					11.0	2.2	5.6	3.6	3.1	
Standard Error		21.0	4.4					4.9	0.97	2.3	1.4	1.3	
Museu Dugès	Female	-	-	-	-	-	-	177[1]	43+[1]	21	13	-	Stickel, 1943
FMNH 39128	Female	169	31	1-1/1-1	7/6	3-4/3-4	8/7	173	36	8	0	7	Present Study; Stickel, 1943
FMNH 39129	Female	201	38	1-1/1-1	7/7	3-4/3-4	8/7	171	39	12	1	9	Present Study; Stickel, 1943
MCZ 33650	Female	272	58	1-2/1-2	7/7	3-4/3-4	6/7	175	46	18	10	6	Present Study; Stickel, 1943
MVZ 45123	Female	253	54	1-3/1-2	7/7	3-4/3-4	6/?	175	45	16	10	4	Present Study
MVZ 76714	Female	228	45	1-1/1-2	8/8	4-5/4-5	7/7	170	40	26	15	8	Present Study
RS 596 HSH	Female	220	36	1-1/1-2	7/7	3-4/3-4	7/7	161	32	16	5	8	Present Study
UIMNH 41688	Female	257	51	1-2/1-2	6/6	3-4/3-4	7/7	177	40	19	9	5	Present Study
UMMZ 109904	Female	192	34	1-2/1-2	6/7	3-4/3-4	6/5	168	37	18	0	17	Present Study
UMMZ 109905	Female	234	41	1-2/1-2	7/7	3-4/3-4	6/7	171	38	20	7	10	Present Study
UMMZ 109906	Female	120	19	1-2/1-2	7/7	3-4/3-4	6/6	171	33	18	16	0	Present Study
Mean		215	40.7					171.2	38.6	17.4	7.8	7.4	
Standard Deviation		45.8	11.7					4.5	4.5	4.7	5.8	4.4	
Standard Error		14.5	3.7					1.4	1.4	1.4	1.7	1.4	

[1] Not included in calculated mean, standard deviation and standard error.

Table 1. Summary of selected meristic and pattern data for the 18 known specimens of *Sonora michoacanensis michoacanensis* (Dugès).

SPECIMEN	SEX	BODY LENGTH MM	TAIL LENGTH MM	NUMBER OF TEMPORALS (LEFT/RIGHT)	NUMBER OF SUPRALABIALS (LEFT/RIGHT)	SUPRALABIALS ENTERING EYE (LEFT/RIGHT)	NUMBER OF INFRALABIALS (LEFT/RIGHT)	VENTRALS EXCLUDING ANAL	CAUDALS EXCLUDING TIP	NUMBER OF GRAY BANDS	NUMBER OF BLACK BANDS NOT SPLIT BY RED	NUMBER OF COMPLETE TRIADS	SOURCE
BMNH 1946.1.14.63	MALE	229	54	-	-	-	-	160[1]	45[1]	12	0	11	STICKEL, 1943; STIMSON, PERSONAL COMMUNICATION
BMNH 1946.1.14.64	MALE	220	48	-	-	-	-	166[1]	46[1]	18	0	17	STICKEL, 1943; STIMSON, PERSONAL COMMUNICATION
AMNH 19714	MALE	247	55	1-2/1-2	7/7	3-4/3-4	6/6	164	42	15	0	13	PRESENT STUDY; STICKEL, 1943
AMNH 19716	MALE	?	43	1-4/1-2	6/7	2-3/3-4	7/6	163	48	15	0	13	PRESENT STUDY; STICKEL, 1943
AMNH 74951	MALE	215	41	? / ?	7/7	3-4/3-4	6/6	171	40	14	0	13	PRESENT STUDY
FMNH 105296	MALE	191	44	1-2/1-2	7/7	3-4/3-4	6/6	163	44	17	2	12	PRESENT STUDY; STICKEL, 1943
FMNH 105297	MALE	189	43	1-2/1-2	7/7	3-4/3-4	6/6	161	44	15	0	14	PRESENT STUDY; STICKEL, 1943
MVZ 71356	MALE	70	15	1-2/1-2	7/7	3-4/3-4	6/6	171	34	13	1	9	PRESENT STUDY
MEAN		194	42.9					165.5	42.0	14.9	0.38	12.8	
STANDARD DEVIATION		48.4	12.4					4.4	4.7	2.0	0.7	2.3	
STANDARD ERROR		18.3	4.4					1.8	1.9	0.7	0.3	0.8	
AMNH 19715	FEMALE	173	31	1-1/1-1	7/7	3-4/3-4	6/6	173	38	31	25	3	PRESENT STUDY; STICKEL, 1943
AMNH ?[2]	FEMALE	-	-	-	-	-	-	173[1]	43[1]	27	23	-	STICKEL, 1943
KU 106286	FEMALE	230	45	1-2/1-2	5/7	1-2/3-4	6/6	178	43	33	32	0	PRESENT STUDY
MCZ 6444	FEMALE	225	40	1-2/1-2	7/7	3-4/3-4	6/6	174+[1]	38	25	26	0	PRESENT STUDY; STICKEL, 1943
UIMNH 18754	FEMALE	210	42	1-2/1-2	7/7	3-4/3-4	6/6	169	41	26	17	6	PRESENT STUDY; STICKEL, 1943
MEAN		210	39.5					173.5	40.0	28.4	24.6	2.2	
STANDARD DEVIATION		16.8	6.0					4.5	2.4	3.4	5.4	2.9	
STANDARD ERROR		9.7	3.0					2.6	1.2	1.5	2.4	1.4	

[1] NOT INCLUDED IN CALCULATED MEAN, STANDARD DEVIATION AND STANDARD ERROR.

[2] SEE TEXT.

Table 2. Summary of selected meristic and pattern data for the 13 known specimens of *Sonora michoacanensis mutabilis* Stickel.

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THE MANDIBULAR DENTITION OF *PLAGIOMENE* (DERMOPTERA, PLAGIOMENIDAE)

Kenneth D. Rose[1]

Abstract. The peculiar bilobate lower incisors and the anterior lower premolars of the Early Eocene genus *Plagiomene* are described for the first time. Several groups of mammals have independently acquired incisors with divided crowns, but available evidence suggests that any resemblances to *Plagiomene,* except in the case of Recent dermopterans, can be attributed to convergence. Nevertheless, the close resemblance between the incisors of *Plagiomene* and those of certain Recent elephant shrews (Macroscelididae) may be indicative of similar incisor function. The hypothesis that Recent dermopterans (Galeopithecidae) are descended from *Plagiomene* or a closely allied form (a view previously based primarily on molar morphology) is strengthened by the specimens described here. A brief review of fossil forms that have been referred to the Dermoptera is presented, and it is concluded that, at present, only two fossil genera, *Plagiomene* and *Planetetherium,* can with reasonable probability be assigned to the Dermoptera.

Introduction

The Early Eocene genus *Plagiomene* has been widely regarded as an early member of the Dermoptera, a view based on the molar morphology, which is similar to that in living dermopterans. Fossil evidence of dermopteran evolution is extremely scarce. Although *Plagiomene* is better known than any other fossil forms that may be considered Dermoptera, it is represented only by dental and gnathic remains. Previous literature on fossil dermopterans (known forms of which are all assigned to the family Plagiomenidae) is minimal, and has been restricted to descriptions of parts of the dentition. None of the anterior dentition has been described or adequately figured before, although the unusual incisors have been noted previously (Jepsen, 1962, 1970; Van Houten, 1945). The nearly complete lower dentition of *Plagiomene* described here (PU 14551, right mandible, and PU 14552, associated left mandible) is significant in providing new evidence that *Plagiomene* is related to and possibly ancestral to extant dermopterans. In addition, an incomplete right mandible, PU 13268, provides the first knowledge of the deciduous premolars in *Plagiomene.*

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Comparative material of *Plagiomene* and other forms has been examined during this study. Abbreviations used in the text are as follows:

AMNH American Museum of Natural History, New York
MCZ Museum of Comparative Zoology (Mammalogy Collection), Harvard University, Cambridge, Massachusetts
PU Princeton University Museum, Princeton, New Jersey
YPM Peabody Museum of Natural History, Yale University, New Haven, Connecticut

DESCRIPTION

The lower dental formula of *Plagiomene,* 3.1.4.3, deduced by Matthew (1918) from fragmentary specimens, is confirmed by PU nos. 14551 and 14552 (see Fig. 1).

The three lower incisors (Figs. 1, 2, 4) of *Plagiomene* are semiprocumbent, with broad, bilobate crowns, of which the mesial lobe is the larger. Faint longitudinal depressions on the lingual sides of these larger lobes in I_1 and I_2 (see Fig. 1 lower) are potential sites for further digitation of the incisor crowns. The crowns are slightly convex on the buccal surface and somewhat concave lingually. The incisors diminish in size from I_1 to I_3, I_1 being considerably larger than I_3. They have an oval, mesiodistally compressed cross section at the root. In the absence of the crowns, Matthew (1918) inferred from the roots that the incisors were small and unspecialized. The specimens discussed here show this inference to have been incorrect. Expansion of the incisors (mostly mesiodistally) occurs at the base of the crowns and increases towards the tip. There are no cingula. A small wear facet on the labiodistal surface of the mesial lobe of left I_1 suggests that upper incisors may have occluded with the lower incisors. This is of interest because in the Recent forms, in

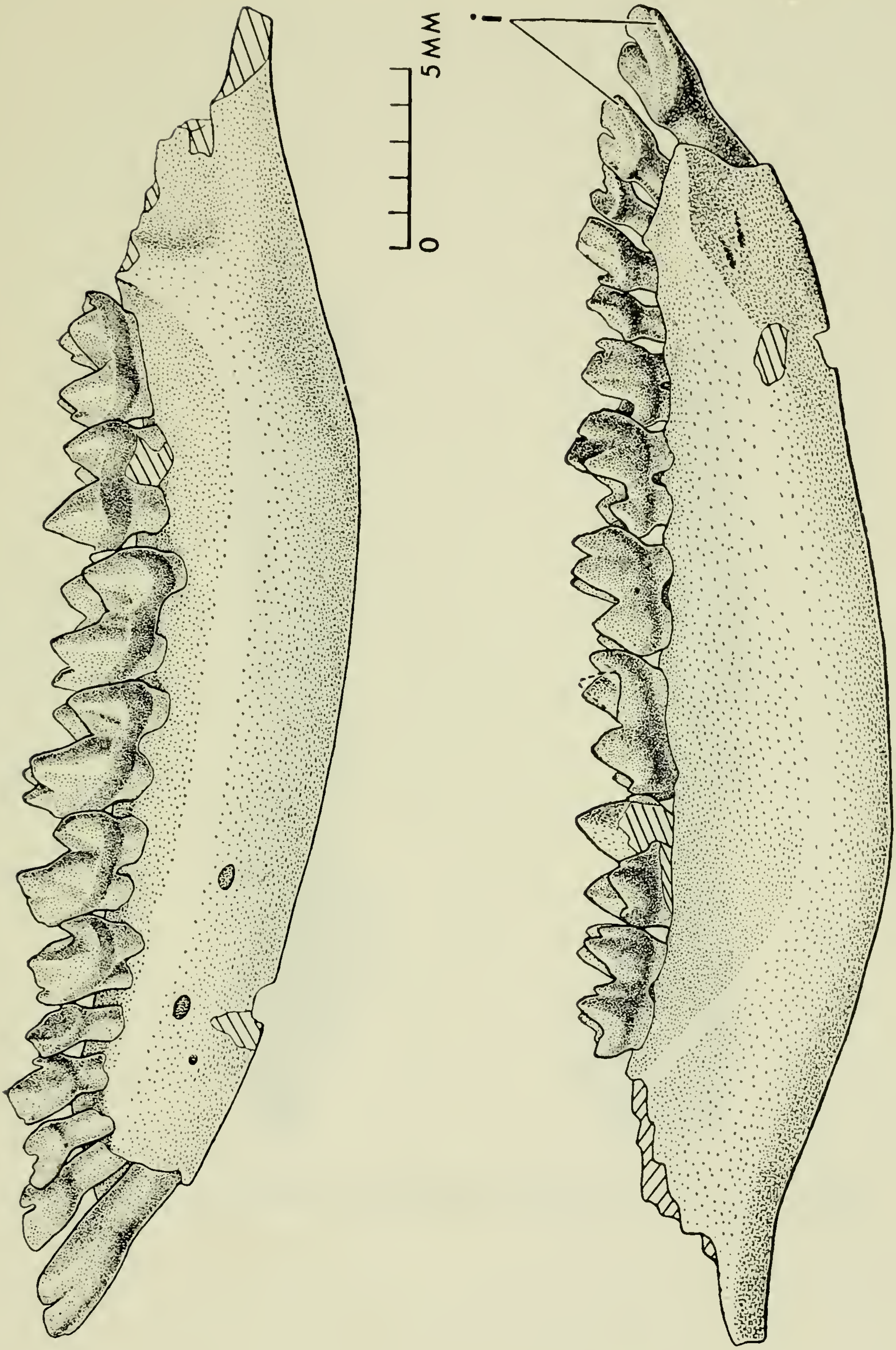

Figure 1. (Upper) *Plagiomene multicuspis* Matthew. Left mandible, PU 14552, lateral view. (Lower) Medial view of same; *i* designates incipient third lobe of I_1 and I_2.

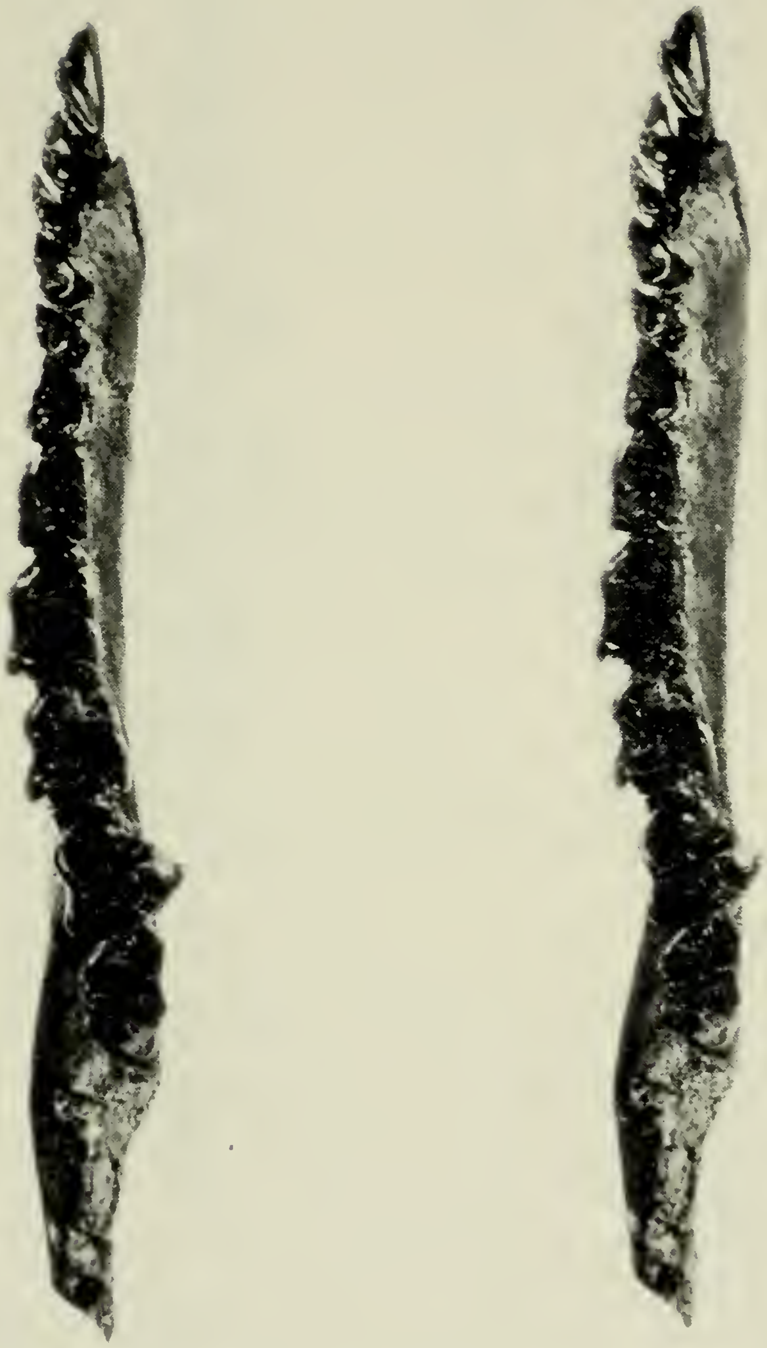

Figure 2. Occlusal view of left mandibular dentition, PU 14552.

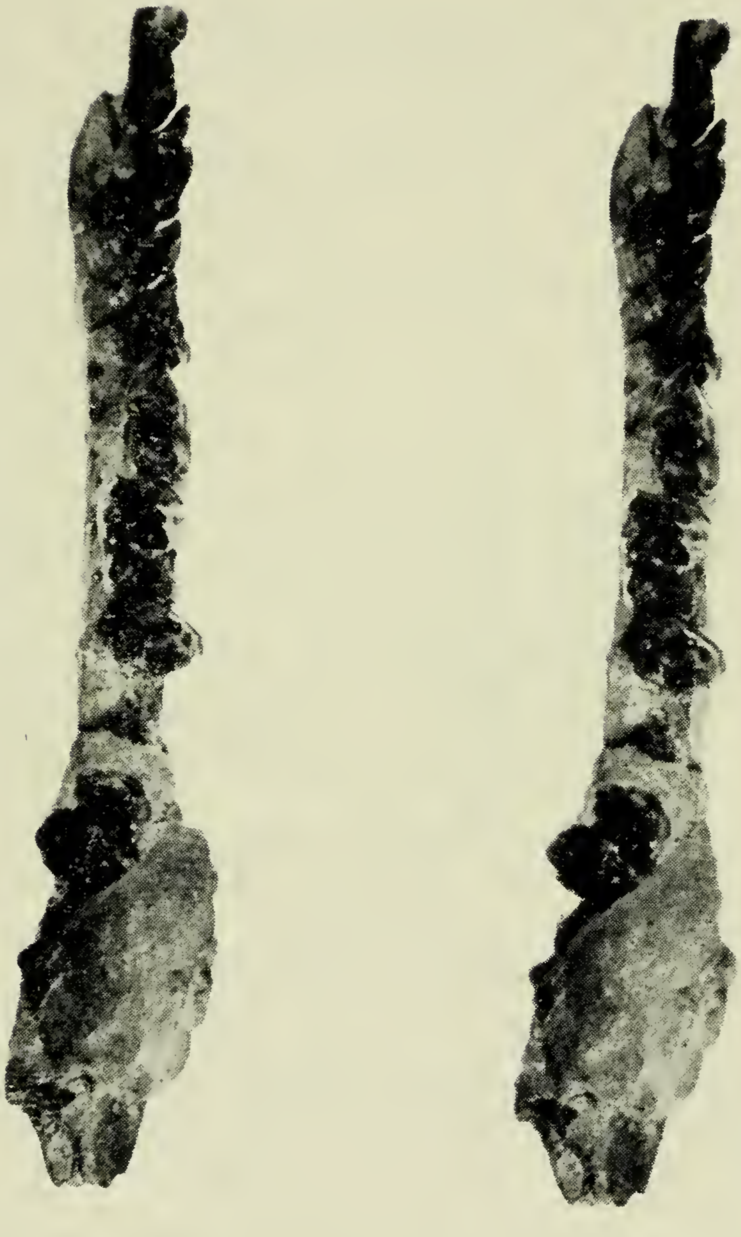

Figure 3. Occlusal view of right mandibular dentition, PU 14551.

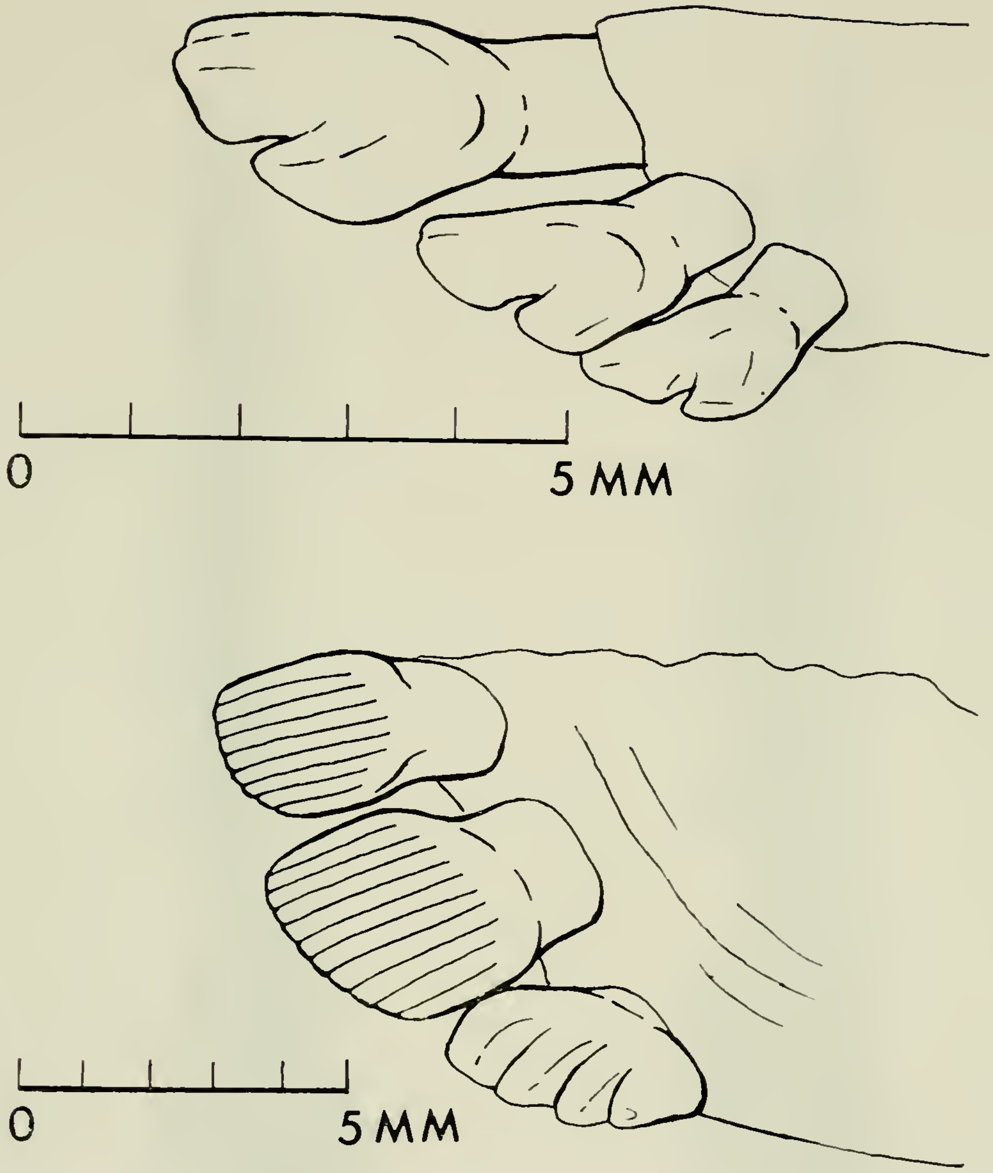

Figure 4. Comparison of lower left incisors (I_1 at top) of *Plagiomene* (above) and *Cynocephalus* (below).

TABLE I

MEASUREMENTS (in mm) OF MANDIBULAR TEETH OF *PLAGIOMENE*

		PU 14552	PU 13268 (Deciduous teeth)
I_1	maximum mesiodistal length	2.3	
	maximum height of crown (measured lingually)	3.4	
I_2	maximum mesiodistal length	2.0	
	maximum height of crown (measured lingually)	2.5	
I_3	maximum mesiodistal length	1.4	
	maximum height of crown (measured lingually)	1.8	
C	maximum length	2.0	
	maximum breadth	1.4	
P_1	maximum length	1.7	
	maximum breadth	1.3	
P_2	maximum length	2.8	2.3 (dP_2)
	maximum breadth	2.0	1.2 (dP_2)
P_3	maximum length	3.7	3.5 (dP_3)
	maximum breadth	2.3	2.0 (dP_3)
P_4	maximum length	4.3	4.3 (dP_4)
	maximum breadth, trigonid	2.8	1.9 (dP_4)
	maximum breadth, talonid	3.2	2.3 (dP_4)
M_1	maximum length	4.3	
	maximum breadth, trigonid	3.0	
	maximum breadth, talonid	3.5	
M_2	maximum length	4.0	
	maximum breadth, trigonid	3.1a	
	maximum breadth, talonid	3.3a	
M_3	maximum length	3.9	
	maximum breadth, trigonid	2.4	
	maximum breadth, talonid	2.4	

a = approximate (tooth damaged)

which I^1 is lost and I^2 is reduced, the anteriormost upper teeth have migrated distally, so that the lower, comblike incisors meet an edentulous area during centric occlusion. The most complete upper dentition known for *Plagiomene,* AMNH 15208 (Szalay, 1969: 241), shows diminishing tooth size anteriorly, however, and does not preserve any incisors (except possibly

I^3). This may indicate reduction or loss of the anterior upper teeth as in extant dermopterans.

The single-rooted lower canine (Fig. 1) of *Plagiomene* is premolariform, consisting of a large anterior cusp, which rises above the crowns of the incisors and of P_1, and a prominent but low heel. A low, incipient cusp is observed on the anterior border. The canine is laterally compressed and its root is elliptical in cross section.

The first premolar is a small, single-rooted tooth bearing one major cusp that may be followed by a much lower, small cuspule. Behind this is a still lower, incipient talonid cusp.

P_2 (Figs. 1–3), a much larger tooth than P_1, is double-rooted and "premolariform-semimolariform" (as defined by Szalay, 1969: 199). The prominent protoconid is preceded by a distinct though much smaller and lower paraconid, which is situated directly anterior to the protoconid (not anterolingual to it, as in the teeth behind P_2). The talonid is much broader and longer than in P_1, but still consists of only a single distinct cusp, homologous to the hypoconid.

The third premolar is semimolariform. The protoconid is the largest cusp, and there is a conspicuous, lower paraconid anterolingual to it. A less prominent metaconid develops from the posterolingual border of the protoconid. Some individuals (*e.g.,* YPM nos. 24966 and 24971) have a small, lower cuspule anterior to the paraconid. The trigonid is somewhat extended anteroposteriorly and there is no trigonid basin. The talonid is well developed, with both hypoconid and entoconid prominent, and with a rudimentary hypoconulid. The talonid basin is closed posteriorly but is open anteriorly in a deep buccolingual valley separating the trigonid and the talonid. This feature is more strongly expressed in the molariform teeth.

P_4 is fully molariform, differing from M_1 chiefly in its slightly smaller size, but these two teeth are frequently almost indistinguishable. The three trigonid cusps and two main talonid cusps of P_4 are large and sharp; the hypoconulid is lower and smaller. Some specimens (*e.g.,* YPM 23578) have a small entoconulid anterior to the entoconid.

The lower molars have been previously figured and described (Matthew, 1918), but a few features may be noted. M_{1-3} are very similar to each other. The trigonid cusps are high and sharp; the metaconid is usually as high as the protoconid or higher, and the paraconid is somewhat lower. In the talonid a

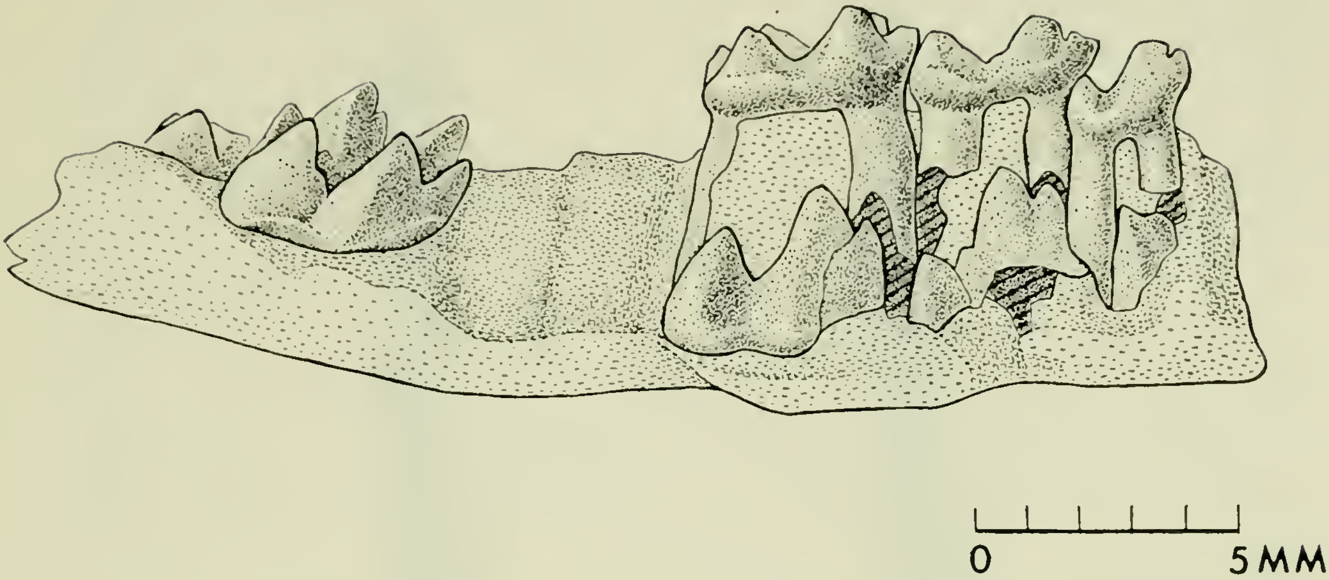

Figure 5. Right mandible with functional deciduous premolars (dP$_{2-4}$) and unerupted permanent P$_{2-4}$; M$_2$ is in process of eruption. Lateral view of PU 13268.

pronounced entoconulid is anterior to the entoconid on M$_2$ and M$_3$, and it is present on M$_1$ in some individuals. Posterior to the hypoconulid, the postcingulid rises in a broad cusplike projection. This is well developed in M$_1$ and M$_2$ and, to a lesser extent, in P$_4$. In M$_3$ the hypoconulid forms a small third lobe. M$_3$ is usually narrower buccolingually than the other molars. The enamel of the molariform teeth is moderately crenulated, particularly in the talonid. A prominent ectocingulid is present on P$_3$–M$_3$ and posteriorly on P$_2$. The posterior premolars and the molars clearly demonstrate a tendency toward polycuspidation, a characteristic of the Plagiomenidae.

The deciduous premolars preserved in PU 13268, dP$_{2-4}$ (see Figs. 5 and 6), are in general similar to their adult replacements. They possess the same cusps in approximately the same positions but are relatively longer anteroposteriorly and more compressed buccolingually. The talonid of dP$_2$ is more molariform than in P$_2$, exhibiting both a hypoconid and a small entoconid. The talonid of dP$_3$ is similarly more expanded than that of the replacing tooth. In the trigonid of dP$_3$ the paraconid and metaconid are somewhat more distinct and better separated from the protoconid than in the permanent P$_3$. In dP$_4$ as well, the talonid is elongated and expanded relative to its condition in P$_4$, and the hypoconulid is much more pronounced, almost forming a small third lobe as in M$_3$.

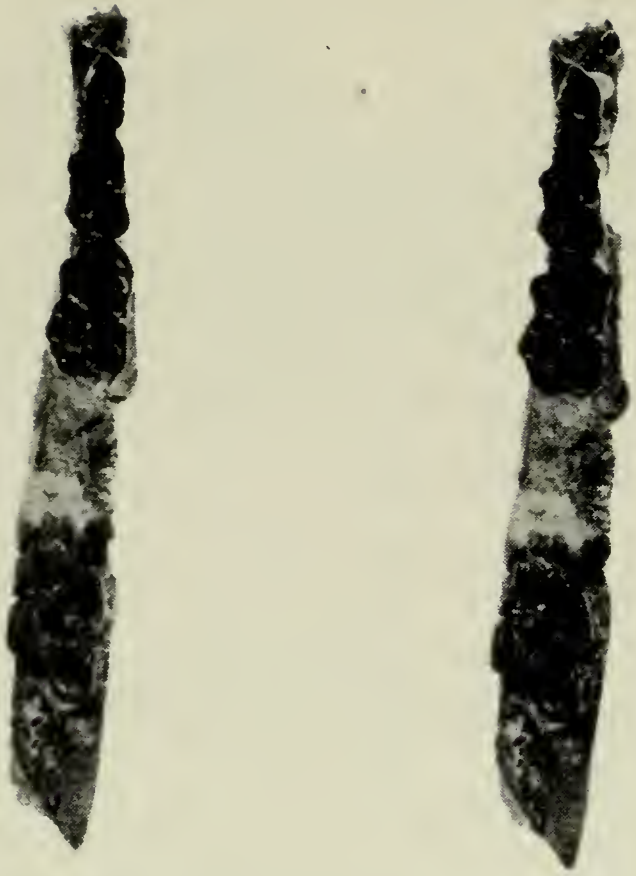

Figure 6. Occlusal view of PU 13268.

DISCUSSION

Incisor specializations comparable to those occurring in *Plagiomene* are found in several other mammals. Incisors with digitate crowns have evolved independently in several unrelated groups, including Carnivora, Notoungulata, Macroscelidea, Dermoptera, and Insectivora. Among these, carnivores such as *Canis* and *Ursus* show tendencies toward digitation of the incisor crowns, but to a less marked degree than in *Plagiomene,* and there is surely no relationship involved. Patterson (1940) described the deciduous incisors of the notoungulate *"Progaleopithecus"* (= *Archaeophylus*), so-named by Ameghino in reference to the dermopteran-like, pectinate incisor crowns, but there is no reason to believe that *Plagiomene* is in any way related to the Notoungulata.

Among the Insectivora, *Nesophontes,* a recently extinct Antillean form (McDowell, 1958: fig. 3), possesses bilobate incisors very similar to those in *Plagiomene. Tenrec* also shows a slight tendency toward digitation of the incisor crowns. There is little resemblance of the lower cheek teeth or the upper dentition of these forms to *Plagiomene,* however. The superficial similarities again may be attributed to convergence.

Certain Recent elephant shrews (Macroscelididae) bear a remarkable likeness to *Plagiomene* in the conformation of the incisors; the most striking examples are *Petrodromus* and particularly *Rhynchocyon*. In the former, the crowns of the permanent incisors are bilobate, while the milk incisors (*e.g.*, MCZ 26113) may have three or four lobes. The lower incisors of *Rhynchocyon* are the closest to *Plagiomene* of any forms examined. They are, however, all approximately of equal size in *Rhynchocyon,* in contrast to the decrease in size from I_1 to I_3 in *Plagiomene*. The remainder of the macroscelidid dentition is quite unlike that of *Plagiomene*. The most obvious contrasts are the loss of M^3_3 (in the majority of known macroscelidids, including both genera mentioned here) and the peculiar structure of the molariform teeth (P^4_4, M^1_1, M^2_2). Macroscelidids are not common in the fossil record, and of those known (Patterson, 1965; Butler and Hopwood, 1957), none show any particular resemblance to *Plagiomene*. The family is unknown outside Africa. Therefore, the similar form of the incisors in some Recent macroscelidids is surely not indicative of any close relationship, although it may reflect functional similarities.

Matthew (1918: 599) noted that the molars of the talpid *Myogale* (= *Desmana*) were of somewhat similar structure to those of *Plagiomene*. Although he viewed this as "perhaps significant of a real though remote affinity" (*ibid.:* 600), the resemblances do not extend to the other teeth. It is unlikely that *Plagiomene* is related to talpids.

Plagiomene has most frequently been compared with the living dermopterans, Galeopithecidae (*e.g.,* Matthew, 1918; Romer, 1966; Szalay, 1969; Jepsen, 1970; among others), and alliance with this group still appears to be the most likely possibility. Matthew (1918) first suggested a relationship between the two groups after studying the molars of *Plagiomene,* which he described as "unlike any placental molars known to me except those of *Galeopithecus*" (*ibid.:* 601). Indeed, the molariform teeth (P^4_4–M^3_3, as in *Plagiomene*) of extant dermopterans show many features in common with *Plagiomene:* prominent conules; absence of hypocone; paracone and metacone situated well lingual to the buccal margin; low paraconid; presence of an entoconulid; talonid and trigonid separated by a deep buccolingual valley; and crenulated enamel. Furthermore, P^4_4 and, to a lesser extent, P^3_3 are molarized as in *Plagiomene*. Although the lower incisors of galeopithecids exhibit less resemblance to those of *Plagiomene* than do most of the forms discussed above, the long time interval separating these two forms must be taken into account. It seems highly probable that the comblike incisors of galeopithecids must ultimately have been derived from incisors with divided crowns such as those present in *Plagiomene* (see Fig. 4). In fact, the form of I_3 in extant dermopterans is an approximate morphologic intermediate between the form of the incisors in *Plagiomene* and the pectinate condition of I_1 and I_2 in the living forms. The dental formula of the Galeopithecidae differs from that of *Plagiomene,* in the loss of two antemolar teeth (probably P_1 and P_2); this is easily explained, however, for the reduction or loss of teeth is common in species that evolve enlarged, specialized teeth, such as the pectinate incisors of galeopithecids. In summary, the new evidence provided by the anterior dentition of *Plagiomene* strengthens the view that it is in or near the ancestry of the Recent Dermoptera.

This view, however, has been questioned recently. Van Valen (1967) regarded the Dermoptera as a suborder of the Insectivora. He suggested (*ibid.:* 271) that the Galeopithecidae may have been derived from *Adapisoriculus* (or an unknown related form) rather than from the Plagiomenidae, which he considered to be "unrelated to the Galeopithecidae" (although including both Plagiomenidae and Galeopithecidae in the same superfamily of the Dermoptera, and placing *Adapisoriculus* in a suborder separate from the Dermoptera).

From the preceding discussion, it is clear that incisors with divided crowns have arisen independently in many unrelated mammals and that such incisors function in various ways. Although incisors of different general morphology are included in this discussion, some of those mentioned above exhibit close resemblances to those of *Plagiomene.* Based on these similarities, incisor function in *Plagiomene* may have been close to that in *Nesophontes, Petrodromus,* and *Rhynchocyon,* and probably not so much like that in extant dermopterans. Unfortunately, little is known of incisor use in any of these forms. Flying lemurs are reported to use their comblike incisors "in scraping the green coloring out of leaves" (Gregory, 1951: 387, quoting H. C. Raven), in ingesting leaves (Winge, 1941), or in grooming (Wharton, 1950). They are strictly herbivorous, feeding mainly on leaves, but including shoots, buds, soft fruit, and coconut blossoms in their diet (Wharton, 1950; Walker et al., 1964; Medway, 1969). In contrast, macroscelidids are primarily insectivorous, feeding largely on ants (Brown, 1964), but almost nothing is known of how macroscelidids use their incisors.

Hiiemäe and Kay (1973) stress that incisors frequently function in processes other than food ingestion and, in fact, that minimal use of incisors during ingestion in primitive mammals provided the opportunity to develop incisor specializations unrelated to feeding. Therefore, it may not be correct to speculate that the diet of *Plagiomene* was similar to that of macroscelidids (indeed, differences in premolar and molar morphology would seem to be against such a supposition); but it does seem likely that in both there are similarities of incisor function.

Fossil forms that have been assigned to the Dermoptera are rare and are represented solely by jaws and teeth. Only two monotypic genera, *Plagiomene* (from the Early Eocene of Wyoming) and *Planetetherium*[1] (from the latest Paleocene of Montana), can with reasonable assurance be referred to the family Plagiomenidae, the only known family (in addition to the Recent Galeopithecidae) referred to the order. *Planetetherium* (Simpson, 1928, 1929; Szalay, 1969) is almost certainly the direct ancestor of *Plagiomene*. It is known from only one locality, the Eagle Coal Mine at Bear Creek, Montana, where it occurs in carbonaceous shale just above the coal layer (Van Valen and Sloan, 1966). The site evidently represents an ancient swamp, and many of the mammals present (including *Planetetherium*) were probably arboreal (Simpson, 1928; Van

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[1] Grassé (1955: 1727, fig. 1698) reproduced drawings of isolated incisors, from Simpson (1928: figs. 12 and 13), and attributed the incisors to *Planetetherium*. This is apparently an unintentional error, which may have occurred because the description of the incisors (which Simpson, p. 14, stated "cannot be definitely classified or correlated with cheek teeth as yet") immediately followed the discussion of *Planetetherium* in Simpson's paper. Simpson believed that the incisors in question belonged to insectivores or primates, but he suggested no association with *Planetetherium*. The morphologies observed differ substantially, indicating that more than one taxon is involved. Inasmuch as *Planetetherium* is the most abundant form at Bear Creek, it seems not improbable that it is among the forms represented by the incisors. Szalay (1972: 25, figs. 1–9) has recently referred one of these incisors, AMNH 22153, to the primate *Carpolestes*, a common occurrence at Bear Creek. There is little evidence to confirm this allocation and, in fact, the morphology of AMNH 22153 may be closer to what might be expected in *Planetetherium* than in *Carpolestes*.

Valen and Sloan, 1966; Jepsen, 1970). *Planetetherium* is by far the most commonly found member of the Bear Creek fauna.

Several isolated teeth from the Early Eocene of France are the basis for a new genus and species being described by D. E. Russell, P. Louis, and D. E. Savage (in press) and regarded by them as a plagiomenid dermopteran. Casts of the teeth show features that suggest to me, however, that the new form may be neither a plagiomenid nor even a dermopteran. More complete evidence may in the future substantiate allocation of this form to the Plagiomenidae, but I do not believe that presently available evidence is sufficiently convincing for such an assignment.

L. S. Russell (1954) proposed *Thylacaelurus montanus* based on a maxillary fragment from the Kishenehn Formation (Late Eocene ?), British Columbia, which he believed to have marsupial affinities. Although the specimen probably represents a placental (McKenna, *in* Van Valen, 1965: 394), Van Valen's (1967) allocation of the genus to the Plagiomenidae is unjustified (see also Szalay, 1969: 242). Its relationships will remain obscure until further material is available.

Van Valen (1967) referred the Mixodectidae to the Dermoptera. This move also seems unwarranted, but the resemblance of *Elpidophorus* to the plagiomenids may be significant. This comparison is not new. Simpson (1936) first discussed this similarity and suggested that *Elpidophorus* provided a suitable structural intermediate between the two families, but he rejected *Elpidophorus* as an ancestor of *Planetetherium* on the grounds that they were approximate contemporaries. This objection is no longer valid, however, for the range of *Elpidophorus* has since been extended back at least into Torrejonian time. Szalay (1969) reviewed the status of relationships between the Plagiomenidae and the Mixodectidae and concluded that available evidence does not support such ties. Nevertheless, the cheek teeth (both upper and lower) of *Elpidophorus* are quite similar to those of *Plagiomene,* sufficiently close to suggest that more than convergence may be involved. It is possible that *Elpidophorus* lies in or near the ancestry of the Plagiomenidae (cf. Sloan, 1969: fig. 6).

The Picrodontidae were placed in the Dermoptera by Romer (1966), but I concur with Szalay (1968: 32) that there is no evidence to support this.

If the Plagiomenidae are truly related to the living flying lemurs, as seems probable on the basis of dental evidence presented above and by Matthew (1918) and Szalay (1969), the Dermoptera have been distinct from other mammalian groups since at least Late Paleocene time. Recent dermopterans have acquired a peculiar suite of specializations (including in particular the dental specializations and the patagium) which is not found in other mammals. In view of these considerations, recognition of ordinal status for the Dermoptera (as accepted by Simpson, 1945; Grassé, 1955; Butler, 1956; Walker, 1964; Anderson and Jones, 1967; among others) seems fully warranted.

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Donald E. Savage kindly sent me a copy of a manuscript (Russell, Louis, and Savage, in press) describing a new form from the Eocene of France. Casts of the new specimens were generously provided by D. E. Russell. I am grateful to Russell, Louis, and Savage for graciously permitting me to include herein a dissenting view on the allocation of this new species.

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MYLOSTOMA VARIABILE NEWBERRY, AN UPPER DEVONIAN DUROPHAGOUS BRACHYTHORACID ARTHRODIRE, WITH NOTES ON RELATED TAXA

WILLIAM J. HLAVIN[1]
and
JOHN R. BORESKE, JR.[2]

ABSTRACT. All known gnathal elements of the durophagous arthrodire *Mylostoma* from the Late Devonian (Famennian) Cleveland Shale of Ohio show that the inferognathal and posterior palatopterygoid elements increase in size and maintain a constant shape during growth, while the anterior palatopterygoids are paired elements in the juvenile condition which fuse into a single median gnathal in the adult. *Dinognathus* is a synonym of *Mylostoma*. *Mylostoma variabile, Mylostoma eurhinus,* and *Mylostoma newberryi* are here considered the only valid taxa. *Mylostoma eastmani* from the Grassy Creek Shale of Missouri (Famennian) is now considered a synonym of *M. variabile;* it was based on undiagnostic gnathal characters. The fusion of anterior gnathal elements is suggested as a possible origin of the median gnathal in the enigmatic arthrodire *Bungartius* and possibly also in the selenosteid *Paramylostoma.*

INTRODUCTION

Newberry (1883: 146) described a left inferognathal from the Cleveland Shale member of the Ohio Shale Formation (Late Devonian, Famennian) as *Mylostoma variabile,* referring to it as a "dipterine ganoid" on the basis of the similarity of its gnathal element to those of *Dipterus* and *Ceratodus.* In 1893, a concretion containing the virtually complete cranial, thoracic, and ventral shield of a single individual was collected from the Cleveland Shale exposures at Brooklyn, Ohio, and was obtained by the American Museum of Natural History, with the counterpart being acquired by the Museum of Comparative Zoology. Dean (1901) described both specimens as *Mylostoma variabile,* placing the taxon within the Arthrodira. Eastman (1906) reviewed the jaw mechanics of *Mylostoma* as well as the morphology of its gnathal elements and concluded that *Mylostoma* was an arthrodire with a gnathal apparatus specialized for crushing.

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Hussakof (1909: 268) described *Dinognathus ferox* as "an imperfectly definable genus and species of arthrodire" on the basis of an isolated median gnathal. Eastman (1909) made a hypothetical reconstruction by placing the *Dinognathus ferox* type of dentition over the inferognathals of *Mylostoma terrelli* and placing the posterior palatopterygoids of *M. terrelli* on the labial side of the *Dinognathus ferox* median gnathal. Dunkle and Bungart (1945) described *Dinognathus eurhinus,* a second species of *Dinognathus,* on the basis of a median gnathal with general morphology differing from that of *D. ferox,* but with features giving evidence for a similar function.

A recently discovered specimen (CMNH 8120) represents a complete set of jaw elements of an adult *Mylostoma variabile.* This specimen, along with other specimens in the Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Oberlin College (OC), and the Cleveland Museum of Natural History (CMNH) has enabled this study of the morphology of the functional region of the inferognathals and palatopterygoids through various size-growth stages. Evidence of the fusion of the anterior palatopterygoids has been observed in the adult, aiding in the synonymy of mylostomatid taxa that were based on undiagnostic character-states of the anterior palatopterygoids.

ORDER ARTHRODIRA

FAMILY MYLOSTOMATIDAE

Mylostoma variabile Newberry, 1883

Mylostoma variabile Newberry, 1883: 146
Mylostoma terrelli Newberry, 1883: 147
Dinognathus ferox Hussakof, 1909: 268
Mylostoma eastmani Branson, 1914: 62

Holotype. OC 1300, left inferognathal.

Paratypes. MCZ 1435, left anterior palatopterygoid; MCZ

1436, right posterior palatopterygoid; AMNH 42G, left anterior palatopterygoid; and AMNH 43G, right anterior palatopterygoid.

Type locality and horizon. Sheffield Lake, Ohio. South Shore of Lake Erie, T 7 N, R 17 W, Lorain County, Ohio; Cleveland Shale member of the Ohio Shale Formation.

Age. Famennian (Late Devonian).

Hypodigm. Cleveland Shale member of the Ohio Shale Formation, Ohio: AMNH 7526, nearly complete disarticulated cranial and thoracic shields (counterpart = MCZ 1490); CMNH 8129, left and right inferognathals, left and right posterior palatopterygoids, median gnathal; AMNH 7915, 10701, CMNH 6094, median gnathals; MCZ 1429–1431, CMNH 5080, 5150, 5177, 6095, 6224, 7256, 7643, 7705, OC 1483, inferognathals; AMNH 44G, 3290, 3588, 3591, MCZ 1437–1438, 13271–13274, OC 1301, 1429, CMNH 5022, 5795, 7694, palatopterygoids. Huron Shale member of the Ohio Shale Formation, Ohio: MCZ 13275, right inferognathal. Grassy Creek Shale Formation, Missouri: University of Missouri collections, median gnathal, posterior palatopterygoid.

Revised diagnosis. Cranial shield having a wide lateral width and short anteroposterior length similar to that of the titanichthyids. Postorbital element bordered posteriorly by paranuchal; centrals not in contact with marginals and are anteriorly separated by pineal. Anterior palatopterygoids of juvenile fuse to form median gnathal in adult. Suborbitals narrow and long, orbits large. Median dorsal short without well-developed keel. Median gnathal of *Mylostoma variabile* possessing a greater width than length and less deeply excavated on either side of the longitudinal ridge than that of *Mylostoma eurhinus*.

SYSTEMATIC DISCUSSION

The holotype of *Mylostoma variabile* Newberry (1883: 146) is a left inferognathal, the size of which indicates that it belongs to a young adult of the species. The paratypes, comprising the anterior and posterior palatopterygoids, are characteristic of the known palatopterygoids of *Mylostoma*. Dean (1901) described the most completely known specimen of *M. variabile* (MCZ 1490, AMNH 7526). This specimen represents a young individual of the species (Plate 1). All of the elements comprising the upper and lower jaw apparatus are well preserved and are the basis for Eastman's (1907) reconstruction of the mylostomatid dentition.

A second species, *M. terrelli* Newberry (1883: 147), represents the left inferognathal (MCZ 1430) of an individual larger than the holotype of *M. variabile.* Hussakof (1909: 268) believed the specific variations in this specimen could be attributed only to an age difference in *M. variabile,* and recommended that *M. terrelli* become a synonym of *M. variabile.*

A third species of *Mylostoma, M. newberryi* Eastman (1907: 224) is based on a pair of dental elements identified as the anterior portions of left and right inferognathals (OC 1302) and the posterior portion of a smaller left inferognathal (MCZ 1439). These dental elements were originally described by Newberry (1889: 165) as belonging to *M. variabile* because of their distinctive narrowness and triangularity, which he believed demonstrated diversity in the species. Earlier, Eastman (1906: 22; fig. E) figured these plates as pre-anterior palatopterygoids as part of his reconstruction of the upper dentition of *M. variabile.* This reconstruction is misleading since these pre-anterior palatopterygoids are not present in the MCZ 1490 and AMNH 7526 specimens. We believe that Eastman realized this a year later and established *M. newberryi* to include these "extra" plates. Morphologically, the dental plates represent the functional region of the inferognathal in a juvenile mylostomatid, having a very thin and narrow attachment with the blade of the inferognathal. This functionally weak attachment between the two areas in this bone may be a result of either an extremely early growth stage or a pathologic condition, the latter being here suggested as an explanation for the abnormal osteological conditions in the jaw elements of the dinichthyid *Hussakofia* (Cossmann).

Branson (1914) described *Mylostoma eastmani* on the basis of an isolated posterior palatopterygoid from the Famennian Grassy Creek Shale of Louisiana, Missouri. This specimen, along with an element referred to by him as an "occipital" (= nuchal) of *Dinichthys rowleyi* (correctly identified as a *Dinognathus*-like median gnathal by Dunkle and Bungart, 1945), comprises the only known occurrence of *Mylostoma* outside the Ohio Shale Formation. The character-states established by Branson (1914) for *Mylostoma eastmani* are undiagnostic since they do not differ from those of *M. variabile,* and we therefore include *Mylostoma eastmani* as a synonym of *Mylostoma variabile.* This occurrence, however, extends the distribution of this genus outside of the Appalachian Basin onto the mid-continent.

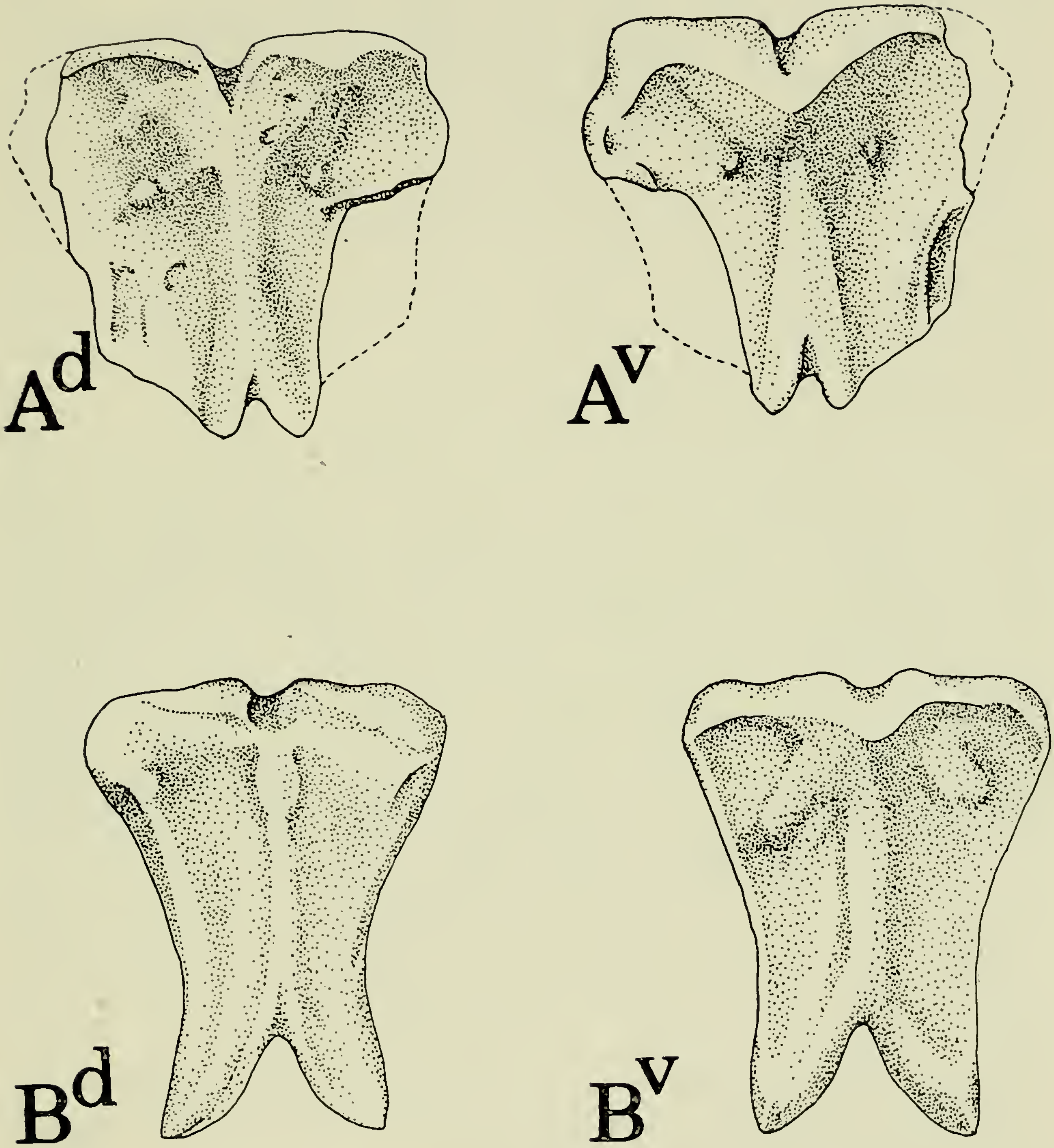

Figure 1. Median gnathal elements (after Dunkle and Bungart, 1945): A, *Mylostoma* (= *Dinognathus*) *eurhinus* CMNH 5063; B, *Mylostoma variabile* (= *Dinognathus ferox*) CMNH 6094; d = dorsal, v = ventral.

Hussakof (1909: 268) described *Dinognathus ferox* (Fig. 1B) from a single median gnathal (AMNH 7915) resembling the mylostomatid dentition but having uncertain affinities. Eastman (1909) felt that *D. ferox* represented the fused part of the anterior palatopterygoids of an adult *Mylostoma,* but he lacked the appropriate specimens needed to prove this hypothesis. Dunkle and Bungart (1945), in describing *Dinognathus eurhinus* from a median gnathal (CMNH 5063; Fig. 1A), did not advocate Eastman's ideas on fusion of the anterior palatopterygoids and opposed his hypothesis on anatomical grounds, which they felt were contradictory to the generalized pattern of jaw elements in all arthrodiran fish. They considered his reconstruction of the *Dinognathus* median gnathal as a dorsal gnathal element of *Mylostoma* to be invalid, arguing that the median gnathal could not have been derived from the fusion of the anterior pair of mylostomatid palatopterygoid elements.

A recently discovered specimen (CMNH 8129; Plate 2) represents a complete set of gnathal elements belonging to an adult *M. variabile.* This specimen consists of typical right and left inferognathals, right and left posterior palatopterygoids, and a *Dinognathus ferox* median gnathal. The discovery of this specimen, which lacks the anterior palatopterygoids but has posterior palatopterygoids and inferognathals associated with the *D. ferox* median gnathal element, confirms Eastman's hypothesis that the median gnathal of *D. ferox* represents the fusion of the anterior palatopterygoids in the adult mylostomatid (Fig. 2). A survey of all known existing mylostomatid palatal dental plates shows them to fall into three size categories: (1) the posterior palatopterygoids, having a size-growth range from juvenile to adult, (2) the anterior palatopterygoids, all representing juvenile specimens of varying degrees but none approaching the adult size of their corresponding posterior palatopterygoids, and (3) the median gnathals or fused anterior palatopterygoids, which all correspond to the adult size of the inferognathals and posterior palatopterygoids of the genus *Mylostoma.*

In view of this evidence, it is suggested here that the taxonomy of the Mylostomatidae may be revised as follows: the genus *Dinognathus* becomes a synonym of *Mylostoma; Mylostoma variabile,* the type species, includes also *Dinognathus ferox, Mylostoma terrelli,* and *Mylostoma eastmani* as synonyms; *"Dinognathus" eurhinus* becomes a valid species of *Mylostoma; Mylostoma newberryi,* a species known only from the anterior portions of its inferognathals, is included within the Mylosto-

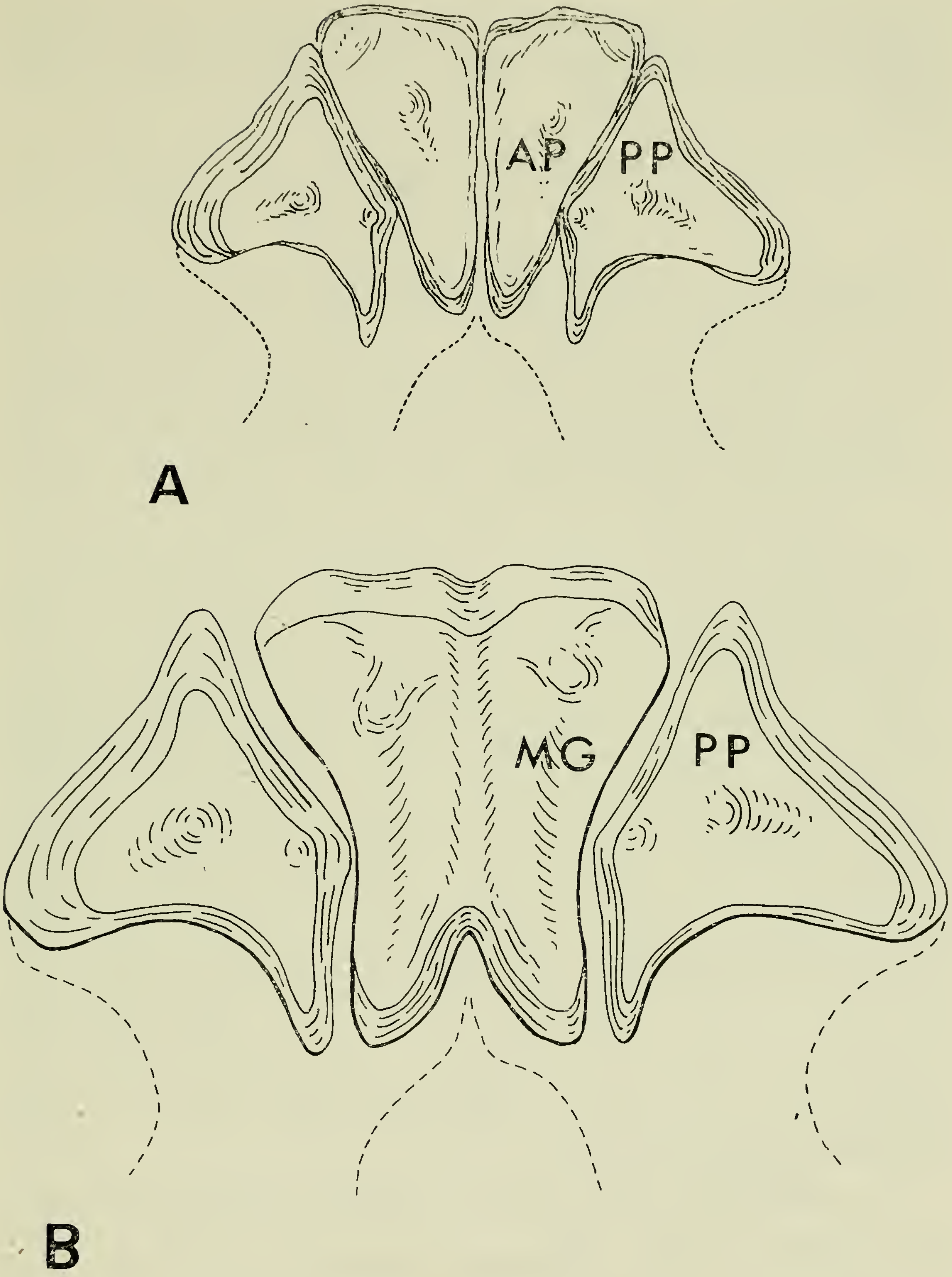

Figure 2. A, Eastman's (1907) reconstruction of the upper jaw apparatus of *Mylostoma variabile,* displaying the paired anterior palatopterygoids (AP) of the juvenile condition (reconstruction based on AMNH 42G-43G, 3591, and MCZ 1437); B, Reconstruction of the upper jaw apparatus of *Mylostoma variabile,* displaying the median gnathal (MG) of the adult condition (fused anterior palatopterygoids; reconstruction based on CMNH 8129); PP = posterior palatopterygoids.

matidae but its affinities with the other species of *Mylostoma* cannot be determined until additional material becomes available.

COMPARISON WITH OTHER ARTHRODIRES HAVING A SIMILAR JAW APPARATUS

As presently constituted, the family Mylostomatidae embraces the following genera: *Mylostoma* (= *Dinognathus*), *Dinomylostoma,* and possibly *Tafilalichthys.* Eastman (1906) described *Dinomylostoma,* which is restricted to the medial Frasnian Shales of New York and Kentucky, as being phylogenetically the most primitive of the mylostomatids. Although incompletely known, it is morphologically and chronologically transitional between *Dinichthys* and *Mylostoma.* The inferognathal elements possess a flat, narrow oral surface, not yet expanded as in *Mylostoma.* The blade-length comprises approximately 45 percent of the inferognathal, displaying the generalized condition of the adductor mandibulae muscles in the Frasnian mylostomatids, as compared to the 60 percent blade-length attained by the arched forward inferognathal elements of the Famennian *Mylostoma.* According to Dunkle and Bungart (1943), this specialized condition increases the length of the adductor mandibulae muscles to produce a more powerful bite. The anterior dorsal gnathal elements of *Dinomylostoma* display features transitional between the dinichthyid anterior supragnathals and the mylostomatid anterior palatopterygoids. The posterior gnathal elements, however, have become completely specialized into well-defined mylostomatid posterior palatopterygoids. This gnathal condition is paralleled to a less specialized degree by the Frasnian pholidosteid *Malerosteus,* described by Kulczycki (1957) from the Holy Cross Mountains of Poland.

It is interesting to note that the enigmatic arthrodire *Bungartius perissus* Dunkle, which is known from a single complete adult specimen, lacks the anterior supragnathal element. The jaw elements preserved represent the corresponding right and left inferognathals, the posterior supragnathals, and a well-developed median gnathal. In this case, Dunkle (1947: 104) considered the "anterior supragnathal element either vestigial or completely absent." The absence of the anterior supragnathal elements in the adult *Bungartius* parallels the absence of these elements in the adult *Mylostoma.* The median gnathal is uniquely restricted to these two genera and we believe it has developed through the fusion of the anterior supragnathal elements during growth. This condition may occur also in the selenosteid *Paramylostoma* Dunkle and Bungart, in which the jaw mechanism is represented by an inferognathal specialized for crushing, and an associated posterior supragnathal. The anterior supragnathal and/or median gnathal is unknown in this genus.

The gnathal condition, suggesting a durophagous habit, while not exclusively restricted to the Mylostomatidae as demonstrated by *Bungartius, Paramylostoma,* and *Malerosteus,* has achieved its highest degree of specialization in the genus *Mylostoma.* This gnathal condition as manifested within other families of arthrodires is believed to represent diverse attempts of broader adaptation and efficiency of the feeding mechanisms at the pachyosteomorph level of organization as suggested by Miles (1969).

On the basis of an isolated cranium, Lehman (1956) described *Tafilalichthys lavocati* as a new brachythoracid arthrodire from the Famennian of Southern Morocco. Obruchev (1964), in his review of this genus, suggested that *Tafilalichthys lavocati* might be a mylostomatid, since the cranium is morphologically similar to that of *Mylostoma* as described by Dean (1901). No gnathal elements are yet known from *T. lavocati,* and therefore no positive assignment to the Mylostomatidae can be made at this time. However, the close relationship of the North American Famennian arthrodiran taxa to the Moroccan arthrodiran remains, as well as a review of the Cleveland Shale Arthrodira, will be of considerable interest in documenting the phylogenetic and paleozoogeographic relationships within the Mylostomatidae.

The stratigraphic range of *Mylostoma* is relatively short, restricted to the Famennian (Late Devonian) time in North America. At this time the brachythoracid arthrodires achieved their highest level of adaptive radiation before extinction.

Acknowledgments

Thanks are due to J.-P. Lehman and Daniel Goujet (Muséum National d'Histoire Naturelle, Paris), Farish A. Jenkins, Jr. and Robert H. Denison (Museum of Comparative Zoology), Richard Estes (Boston University), and William E. Scheele (Cleveland Museum of Natural History) for their helpful suggestions. This research was supported in part by grants from the Albion Foundation and Sigma Xi to Hlavin.

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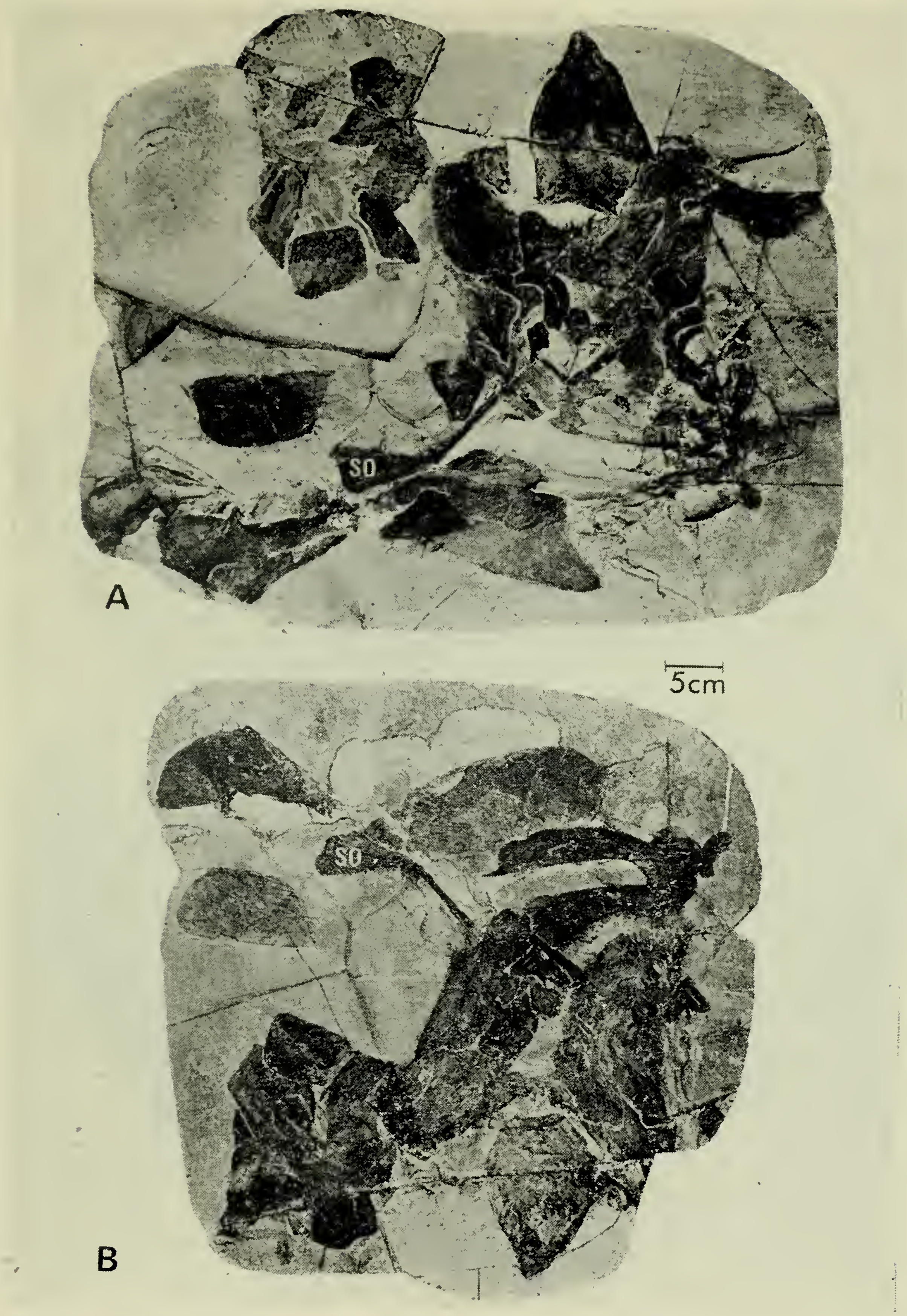

Plate 1. *Mylostoma variabile* (displaying cranial, thoracic, and ventral shields), juvenile: A, MCZ 1490; B, counterpart AMNH 7526; SO = suborbital.

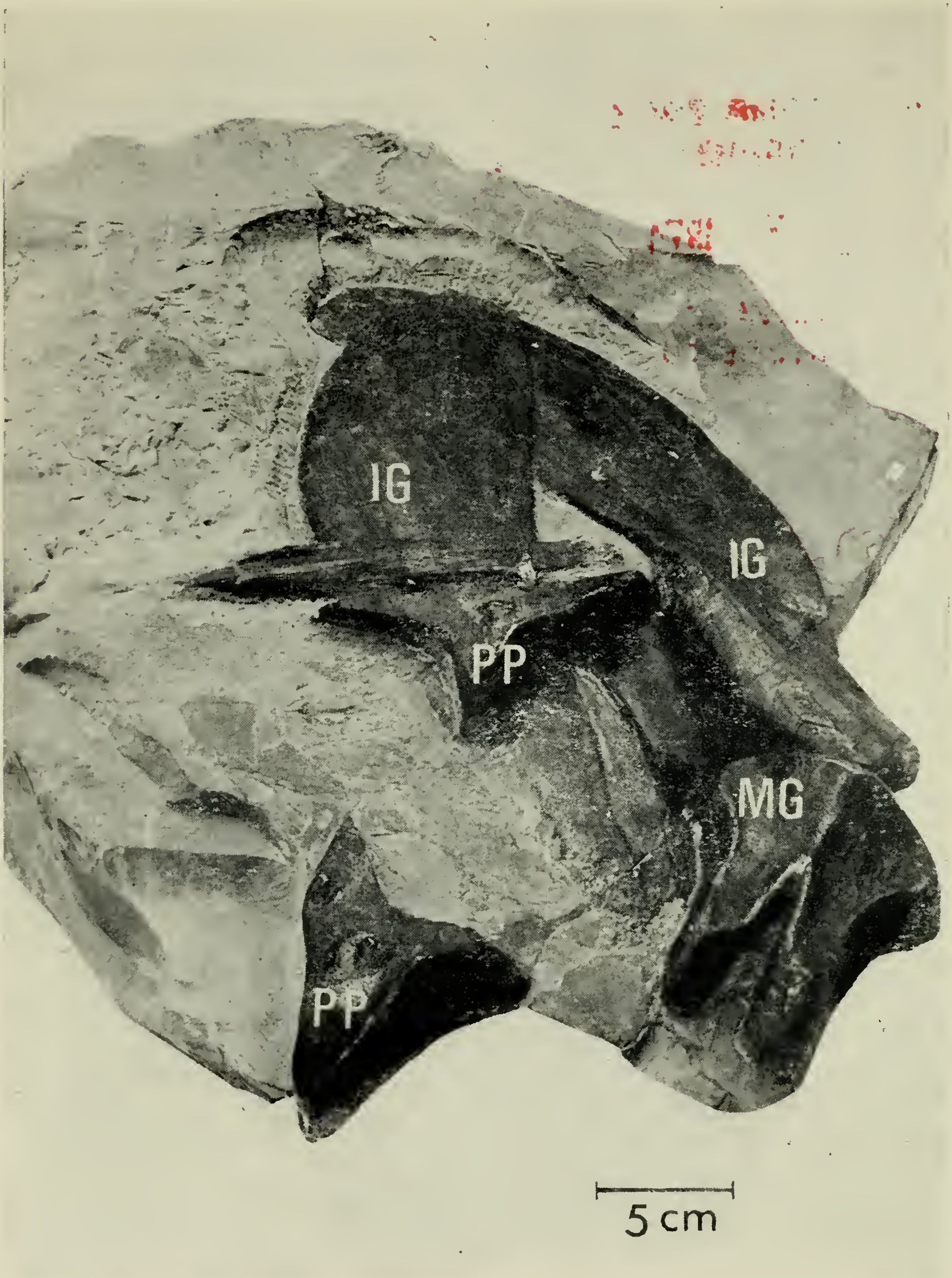

Plate 2. *Mylostoma variabile* CMNH 8129; jaw elements of an adult showing left and right inferognathals (IG), left and right posterior palatopterygoids (PP), and a median gnathal = fused anterior palatopterygoids (MG).

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

XX. SUMMARY

Alfred Sherwood Romer

Abstract. A brief account is given of the geologic setting of the Triassic tetrapod faunas found in South America; the nature of the Chañares reptile fauna is summarized, and this fauna is compared with other Triassic assemblages in South America and other continents.

In nineteen previous papers in the Museum of Comparative Zoology *Breviora*[1], an account has been published of the reptile fauna from the Triassic Chañares Formation of Argentina collected by the La Plata-Harvard expedition of 1964–65; this series includes, in addition to papers written by myself, contributions by C. Barry Cox, Farish A. Jenkins, Jr., James A. Jensen, and Arnold D. Lewis. Except for a future detailed study of the skull of the cynodont *Probainognathus* by Edgar F. Allin and myself I have no further plans for publication on the Chañares fauna. The present paper is intended to furnish a short summary of the results of the 1964–65 expedition. Except for a few forms recently described from the Chañares Formation, a recent paper by Bonaparte (1972) gives a succinct summary of all known reptiles from the South American Triassic, so that detailed references are unnecessary below.

As noted in previous papers in this series, I am deeply indebted to the National Science Foundation for grants for collection, preparation, and publication of the Chañares fauna.

Geologic Setting

Until the last few decades, almost nothing was known of the

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[1] Breviora Nos. 247, 252, 264, 295, 333, 344, 352, 373, 377, 378, 379, 385, 389, 390, 394, 395, 396, 401, and 407.

Triassic tetrapod faunas of South America. Now, however, tetrapods are known from five discrete areas of Argentina and southern Brazil:

(1) The El Tranquilo Formation of Santa Cruz Province of Patagonia. From the upper part of this formation, obviously of Late Triassic age, have been collected prosauropod dinosaur remains. These have been studied by Casamiquela, but the results have not been published; they appear to pertain to the European genus *Plateosaurus*.

(2) The Puesto Viejo Formation, in southern Mendoza Province. Undescribed fragmentary remains are present in the lower part of the formation; from the upper part, Bonaparte has described a primitive but somewhat specialized traversodontid gomphodont *Pascualgnathus* and, most interestingly, forms indistinguishable from *Cynognathus* and *Kannemeyeria,* the most characteristic genera of the *Cynognathus* zone of the Upper Beaufort beds of South Africa. The Scythian age of this formation is obvious.

(3) The Cacheuta Basin. In the precordillera west of Mendoza is a series of beds of Triassic age, the Cacheuta Series. I have elsewhere (Romer, 1960) given a brief resumé of the geology. Four formations have long been recognized; in ascending order they are the Las Cabras, Potrerillos, Cacheuta and Río Blanco; recently a basal Río Mendoza Formation has been distinguished. Rusconi, in various publications (as Rusconi, 1951) has described vertebrates from these beds, including various fishes, many of uncertain systematic position, and from the Cacheuta Formation, flat-skulled amphibians of the genus *Pelorocephalus* [*Chigutisaurus*], which, although comparable in many regards to the brachyopids of other Gondwana continents, appears not to pertain to that group. Reptilian remains are rare; in the older collections there was, apart from a few scraps, only the postcranial skeleton of a primitive thecodont, *Cuyosuchus.* More recently an indeterminate jaw from the Potrerillos Formation has been described as *Colbertosaurus*, and Bonaparte has described the gomphodonts *Andescynodon* and *Rusconiodon* and a kannemeyeriid dicynodont, *Vinceria* from the Río Mendoza Formation. Because the flora of the Cacheuta Series is of the *Dicroidium* type present in the Late Triassic, Stipanicic (1969) believes the Cacheuta beds to be relatively Late Triassic in age. However since the *Dicroidium* flora extends well down toward the level of the Upper Beaufort beds of South Africa, Bonaparte's belief (1966, etc.) that part of the Cacheuta Series is

relatively Early Triassic in age is reasonable. Unfortunately the reptile fauna is as yet too fragmentary in nature for adequate comparisons to be made.

(4) Santa Maria Formation. From this Triassic formation in southern Brazil a few bones were early sent to the British Museum; major collections were later made by and for Huene, whose full results were published in 1944; further collections have been made by Price and White for Harvard University, by Colbert for the American Museum, and by Price for the Brazilian Geological Survey. The Santa Maria Formation has been described by Beltrão (1965) and by Bortoluzzi and Barbarena (1967). The vertebrate remains are confined to the upper part of the formation, and there is no known difference in the age of the beds between the three major collecting areas — near the city of Santa Maria, in the region of Chiniqua, west of that city, and in the Candelaria region, well to the east.

The fauna is varied, but the nature of preservation is such that structural details are frequently obscure and many forms are imperfectly known. Included are the procolophonid cotylosaur *Candelaria;* the rhynchosaur *Scaphonyx* [*Cephalonia*]; a number of thecodonts including *Cerritosaurus, Rauisuchus, Prestosuchus, Hoplitosuchus, Procerosuchus;* a fragmentary postcranial skeleton that appears to be a primitive saurischian, *Staurikosaurus* and a questionable second dinosaur, represented by a few vertebrae and limb bones; two carnivorous cynodonts, *Chiniquodon* and *Belesodon;* the gomphodont cynodonts *Traversodon* and *Gomphodontosuchus;* the dicynodonts *Barysoma, Dinodontosaurus* and *Stahleckeria.*

As discussed later, the Santa Maria Formation seems surely to be equivalent to the Los Rastros Formation of the Talampaya basin.

(5) The Talampaya basin or Villa Uníon-Ischigualasto cuenca. This is the largest and most richly fossiliferous of the bone-bearing South American Triassic areas. It lies on the boundary between La Rioja and San Juan provinces, between the Sierra de Sañogasta on the east and the Ríos Bermejo and Guandacol on the west, and extends from the region of Villa Uníon on the north to the Sierra de Valle Fertil on the south. Faults are numerous, but in general the Triassic beds can be grouped in two areas, east and west of the flat alluvium-covered Talampaya plain, the two areas being essentially the two limbs of a major syncline, with various formations present in reverse order on the two sides of the plain. The area to the west of the

plain is the better known and here the formations identified are much thicker than on the east: This region was explored by earlier geologists, but first adequately studied by Frenguelli (1946); his account has been modified and corrected by later workers, such as Groeber and Stipanicic (1953) and Ortíz (1968). To the northwest, in the region of Cerro Bolo there is an exceedingly thick series of beds that appear to extend continuously upward from the Carboniferous "Paganzo I" to the Late Triassic; this region was studied by de la Mota, whose work, unfortunately, remains unpublished. To the southwest the series, as far as published results are concerned, terminates below in the presumed Triassic "Paganzo III." For much of the western border this last is absent; if included, the major formations, in descending order, are:

Los Colorados Formation,
Ischigualasto Formation,
Los Rastros Formation,
Tarjados Formation (= Paganzo III).

As described by Frenguelli, the Los Colorados beds were termed the Gualo Formation, a mistake corrected by Groeber and Stipanicic. The lower part of the Los Rastros Formation was synonymized by Frenguelli with the Ischichuca Formation; as pointed out by Ortíz this is incorrect, for the type Ischichuca, in the Cerro Bolo region, is synonymous with the main carbon-bearing beds of the Los Rastros. The lowest redbeds were thought by Frenguelli to represent the Permian "Paganzo II," whereas, as Ortíz states, they are the redbeds of "Paganzo III," or Tarjados.

Fragments of vertebrate skulls were recovered by Frenguelli from the Ischigualasto Formation and described by Cabrera in 1943. The richness of fossils in this formation was disclosed by the Harvard-Buenos Aires Museum expedition of 1958 (Romer, 1966). For many years, from 1958 on, the Ischigualasto beds were worked by expeditions from the Instituto Lillos of Tucumán, at first under O. A. Reig, later with great success by J. F. Bonaparte. The rich reptile fauna includes the rhynchosaur *Scaphonyx;* the thecodonts *Proterochampsa, Saurosuchus, Venaticosuchus, Triassolestes, Aetosauroides* and *Argentinosuchus;* the rare saurischian dinosaurs *Herrerasaurus* and (?)*Ischisaurus;* the ornithischian *Pisanosaurus;* fragmentary remains perhaps representing the carnivorous cynodont *Chiniquodon;* the gomphodonts *Exaeretodon, Proexaeretodon* and *Ischignathus;* the dicynodont *Ischigualastia.* Except for representatives of Ischigualasto forms in transitional beds, no reptiles are known from the Los Rastros beds or the underlying Tarjados Formation. Above the Ischigualasto Valley rise the high cliffs of the Los Colorados. Except for a single dicynodont, *Jachaleria,* the faunal content of most of the thick series of Los Colorados redbeds is unknown; from the few meters available at the summit of the cliffs Bonaparte has described (1972b) a fauna of very late Triassic age, including the thecodonts *Riojasuchus, Pseudhesperosuchus* and *Neoaetosauroides;* the primitive crocodilian *Hemiprotosuchus;* the prosauropod *Riojasaurus;* and fragmentary materials comparable to *Tritylodon.*

We are here concerned mainly with beds lying to the eastern side of the basin, which was little studied by earlier workers; Jensen and I (1966) have discussed the geology here. Most of the formations present can be matched with those on the west side of the valley, although they appear to be much thinner here. The formations present (all adequately represented along the course of the Arroyo de Agua Escondida) are, in descending order:

Los Colorados Formation,
Ischigualasto Formation,
Los Rastros Formation,
Chañares Formation,
Tarjados Formation,
Talampaya Formation.

These formations are presumably underlain by the Carboniferous and Permian beds of "Paganzo I" and "Paganzo II," which are exposed on the slopes of the Sañogasta Range, east of a major north-south fault at the western margin of the mountains; in the area studied, however, we have not seen a contact between "Panganzo II" and the base of the Talampaya beds. The latter formation is best exposed in the cliffs forming the walls of the "Puerta de Talampaya," where 180–200 meters of these beds are present. They mainly consist of soft sandstones, but with occasional "cobbles." No fossils of any sort have been found. They appear to be purely continental in nature and are not improbably Early Triassic in age, or possibly Late Permian.

Unconformably above the Talampaya beds are the hard sandstones of the Tarjados Formation, some 385 meters in thickness at the Arroyo de Agua Escondida. These beds correspond, apparently, to part or all of the sandstones elsewhere termed

"Panganzo III." For the most part they are red, but in the southern part of the area studied the upper beds are white in color. Fossils are rare, but a few fragmentary dicynodont remains have been found in the upper layers. They are presumably Early Triassic in age.

On the irregular upper surface of the Tarjados sandstones lie unconformably the 75 meters of the volcanic ash deposits constituting the Chañares Formation. The uppermost layer of the Tarjados, about half a meter thick, forms an uneven, undulating surface of hard resistant materials suggesting hydrothermal action. Obviously there was major volcanic activity in the region at that time. The Chañares sediments show none of the layering that would be expected if the ash had been laid down in water; presumably there was merely a covering of the then existing surface with tremendous quantities of volcanic ash in Pompeii-like fashion. Bearing out such a conclusion is the fact that no trace of water-dwelling amphibians or fishes have been discovered in the Chañares and — more significant — almost all the numerous reptile remains found are in the lowest few meters of the ash deposits. Apparently the ash falls resulted in the local extermination of the vertebrate fauna.

As Jensen and I noted in 1966, it is not customary in Argentina to give a formation name to a set of beds of such limited thickness. I believe, however, that it is warranted in this case because of the distinctive nature of the sediments, and most especially, because of the vertebrate fauna contained in them.

Bonaparte (1967) suggested that the Chañares beds are equivalent to those of the Ischichuca Formation, the type section of which lies in the Cerro Bola region. However, both Ortíz (1968) and I (1971) have shown that this is incorrect. Bonaparte informs me that light-colored beds, which may be comparable to those of the Chañares, are present below the typical Los Rastros in the southwestern part of the basin, and that he has collected reptiles of Chañares type there. I have not visited this area. Ortíz includes these beds in the Los Rastros Formation, and if one does not wish to distinguish a separate Chañares Formation, one might include it in the Los Rastros — despite the marked contrast in the nature of the sediments — but could not, of course, consider these beds as part of the so-called "Ischichuca."

Conformably above the Chañares ash beds are the Los Rastros sediments of shales, clays, and sandstones, with intercalated carbonaceous layers, similar in nature to the beds of this formation in the western part of the basin. Because of numerous faults it is impossible to determine the thickness of the Los Rastros in this region, but it is obviously much less than the estimated 600 meters found west of the Ischigualasto Valley.

Only a limited exposure of Ischigualasto Formation sediments is present in this region; the thickness observed is but 175 meters, as compared with 400–500 meters in the type area. Above the Ischigualasto Formation are present Los Colorados beds, only 95 meters thick; whether this is the total amount originally deposited or whether they were originally thicker and later reduced by erosion before deposition of overlying Tertiary sediments is uncertain.

The Chañares Fauna

Below are listed the reptiles discovered in the 1964–65 expedition and described in earlier papers in this series. A few forms are represented by fairly complete specimens; others are known only from fragmentary materials. Much further collecting is possible; one may hope that if and when such collecting can be done, much better material of many of the forms already described may be obtained and additions be made to the faunal list:

Dicynodonts:
  Chanaria platyceps
  Dinodontosaurus brevirostris
  Dinodontosaurus platygnathus
  Kannemeyeriid indet.
Gomphodont cynodonts:
  Massetognathus pascuali
  Massetognathus teruggii
  Massetognathus major
  Megagomphodon oligodens
Carnivorous cynodonts:
  Probelesodon lewisi
  Probelesodon minor
  Probainognathus jenseni
Thecodonts:
  Luperosuchus fractus
  Lagerpeton chanarensis
  Lagosuchus talampayensis
  Lagosuchus lilloensis
  Chanaresuchus bonapartei

Gualosuchus reigi
Gracilisuchus stipanicicorum
Lewisuchus admixtus

Dicynodonts. In contrast to the wealth of dicynodonts in the later Permian, the group in the typical Triassic deposits is restricted to a few forms of relatively large size (their place as herbivores appears to have been taken over mainly by rhynchosaurs and gomphodonts). In the Chañares beds such forms are present, but only in modest numbers, dicynodont specimens constituting but perhaps 5 percent or so of the total of reptiles collected. A few postcranial remains suggest the presence of a kannemeyeriid; apart from this, three types of dicynodonts are present, all of which are assigned by Cox to the characteristically Middle Triassic family Stahleckeriidae — *Chanaria platyceps, Dinodontosaurus platygnathus,* and *D. brevirostris. Chanaria* is a form not present elsewhere; however, the *Dinodontosaurus* species are quite similar to the genotypic form from the Santa Maria Formation (presumably of somewhat later age).

As also mentioned below, ecologic factors tend to separate stratigraphically and topographically the three common herbivore groups — dicynodonts, gomphodonts and rhynchosaurs — of the South American Middle Triassic fossiliferous areas. In the Santa Maria beds, dicynodonts and rhynchosaurs are, so to speak, "allergic" to one another; rhynchosaurs abound in the deposits near Santa Maria city but are unknown in the two other major fossil beds in this formation where dicynodonts are abundant. At Ischigualasto all known dicynodonts have been found in a stratigraphically narrow band, about half-way up the formation, and quite distinct from higher levels where gomphodonts abound, and from lower levels where rhynchosaurs are plentiful. In the Chañares beds, as noted above, almost all fossils are from the lowest part of the formation, but I have the impression that all dicynodonts collected were from the very base, within a meter or two of the unconformity with the Tarjados sandstones, whereas other types tended to occur up to a dozen or so meters higher.

Gomphodonts. Gomphodont cynodonts are the dominant herbivores in the Chañares beds; more than half of all specimens collected in the 1964–65 expedition were members of this group. Nearly all clearly pertain to a single genus, *Massetognathus.* In the first box of fossils received in Cambridge, Massachusetts, there was present a considerable series of specimens that seemed to sort out clearly into two size groups, and hence I described them as belonging to two species, *M. pascuali* and *M. teruggii.* As I noted later, the full collection, when received, broke down such a clear distinction. Dr. James Hopson tells me that in primitive African cynodonts which he has been studying, a very considerable size range is to be found; this suggests that *M. pascuali* and *M. teruggii* merely represent populations of two sizes of the same species. However, as my tables show, the size distribution is heavily weighted above the peak that one may reasonably believe to represent mature adults, and the presence of two common species of *Massetognathus* is still a not unreasonable assumption. Still further, the size range of specimens that seem to belong to this genus is such that I find it impossible to believe that the amount of growth necessary to reach the size of the largest specimen can have been possible if a single species (or even two species) had been present, and hence have with some confidence given the name *Massetognathus major* to this relatively enormous skull.

Nearly all the gomphodonts in the collection appear to be reasonably assignable to a single genus. However, two rather large individuals are clearly distinctive, and I have given the name *Megagomphodon oligodens* to this rare form.

The Chañares gomphodonts are clearly members of the family Traversodontidae, a group to which all known South American gomphodonts belong (and also forms present in the Manda beds of East Africa). In the Santa Maria beds of Brazil gomphodonts are less common, and are represented mainly by the genus *Traversodon.* This genus may well have descended from *Massetognathus,* but its remains are too poor to allow a detailed comparison. The Ischigualasto traversodontids are obviously much more advanced types.

Rhynchosaurs. Quite as significant as the presence of certain forms in a given formation is the absence of expected types. Most Triassic reptile faunas, except those of the very earliest and very latest parts of the period, are notable for the presence of rhynchosaurs, often in great abundance. In our Chañares collections there is not the slightest trace of a rhynchosaur (despite the fact that identifiable elements of this type of animal, most especially upper tooth plates, are readily preserved and readily recognized).

Why are no rhynchosaurs present? It is not because they had not yet evolved, for although the Chañares beds date from a fairly early time in the Triassic, primitive rhynchosaurs were already present in the *Cynognathus* Zone, definitely earlier, and were abundant in the Manda beds of East Africa, which (as discussed later) are probably somewhat earlier than the Chañares Formation. Quite certainly rhynchosaurs had evolved by the time of formation of the Chañares beds and (although there is no proof) may have been present in Argentina at that time.

Their absence here is quite surely, as I have suggested elsewhere (Romer, 1973), attributable to some ecologic factor. Rhynchosaurs and gomphodonts, in South American deposits at least, seem to be basically incompatible.[1] In the Ischigualasto beds, rhynchosaurs are exceedingly abundant in the lower part of the formation, but in our 1964–65 expedition we found no specimens in the upper half of the beds. On the other hand, on our expedition we found gomphodonts to be very rare in the lower part of the Ischigualasto Formation but very abundant in the upper half of these deposits. Rather surely the contrast is related to the type of plants present; the rhynchosaurs fed on some type of plants having a hard-shelled "seed" for which the "cracking" dentition of these forms was a necessity; the gomphodonts, as the grinding character of their teeth and the absence of a cracking device indicate, fed upon some different types of plant materials. In the Santa Maria Formation, gomphodonts are not as conspicuous as in the Ischigualasto and Chañares beds, but such gomphodonts as are present there are absent in the beds near Santa Maria city where rhynchosaurs alone are present. If, as is probable, rhynchosaurs were present in South America in Chañares times, they would presumably have been of a relatively primitive type, comparable to *Stenaulorhynchus* of the Manda beds rather than the more advanced genus present at Santa Maria and Ischigualasto.

Carnivorous cynodonts. In the Permian and earliest Triassic the typical carnivores are therapsids; during the Triassic carnivorous therapsids are reduced and disappear, to be replaced by archosaurs (but giving rise to the earliest mammals before disappearing completely). In the Chañares beds, thecodont archosaurs were becoming abundant, but carnivorous cynodonts were still present and modestly abundant. They are interesting in being more advanced than *Thrinaxodon* and *Galesaurus* of the earliest Triassic and without the somewhat specialized features seen in *Cynognathus,* the common form in the Late Beaufort of South Africa. *Probelesodon lewisi* is quite clearly ancestral to

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[1] Charig tells me, however, that there is no evidence for this in the Manda beds of East Africa.

Belesodon of the somewhat later Santa Maria beds; apparently two species are present, *P. lewisi,* fairly common, and a smaller form, *Probelesodon minor.* More interesting is *Probainognathus,* in which a startling advance is the presence of a socket — a glenoid cavity — in the squamosal for attachment of the jaw. This, however, is only a half-way stage in the development of the mammalian system of jaw suspension, for this glenoid is for the reception of an articular body of the lower jaw formed by a fusion of the posterior elements of the reptilian jaw type; the dentary bone, which in mammals articulates with the squamosal, is as yet not quite in touch with the squamosal. The teeth of *Probainognathus* are usually worn and show only the main fore-and-aft row of cusps present in the teeth of primitive mammals and seem to lack the row of basal "cusplets" found in early mammals. For this reason it was thought for a time that *Probainognathus* could not be on the direct line of ascent to mammals. However, Hopson has studied a little-worn dentition in which these cusps are present and hence it may be reasonably considered to be a true pre-mammal, or at least very close to the actual ancestral line.

Thecodonts. Although carnivorous cynodonts still survived, thecodonts were well on their way toward succeeding them as dominant carnivores. In earlier years we knew little of this group except for a few primitive forms in the Early Triassic and (apart from the specialized phytosaurs) only a few survivors in the Late Triassic, where the thecodonts were already being succeeded by the dinosaurs descended from them. One could have reasonably assumed that were Middle Triassic beds well known, the thecodonts would be discovered to be a varied group, with a variety of forms leading in different directions — toward pterosaurs, bird ancestors, crocodilians and dinosaurs. Our increased knowledge of Middle Triassic fossil deposits in recent decades has gone far toward verifying this assumption, for although many phyletic lines are far from clear, it is obvious that during the middle part of the Triassic the thecodonts were undergoing a rapid radiation into a wide diversity of types. The only large Chañares form is *Luperosuchus,* represented only by an incomplete skull, which appears to be a member of the prestosuchid (or rauisuchid) assemblage, of uncertain relationship. No close affinities are known for *Lewisuchus* or the two small long-legged types, *Lagosuchus* and *Lagerpeton,* represented mainly by hind legs. *Chanaresuchus* and *Gualosuchus* are long-snouted, probably amphibious forms related to *Cerritosaurus* of the Santa

Maria and *Proterochampsa* of Ischigualasto; once suggested as crocodilian ancestors, the proterochampsids do not seem to be related to that group, but are not impossibly related to the phytosaur pedigree. A progressive form is *Gracilisuchus,* related, it would appear, to *Ornithosuchus* of the later Triassic, which has suggestive resemblances to primitive theropods, although it is far from certain that the ornithosuchids are ancestral to these dinosaurs. The Chañares thecodonts, as was stated, increase considerably our knowledge of thecodont diversity, but as yet do little toward establishment of any major archosaur evolutionary lines.

Comparison With Other Faunas

As knowledge of Middle Triassic faunas has increased, ideas as to the stratigraphic position and interrelations of these faunas have been expressed by a variety of workers, such as Bonaparte, Colbert, Cox, Reig, and myself. I shall here merely consider the interrelationships of these faunas from the point of view of the Chañares assemblage. I have recently reviewed the Triassic faunas in a plenary paper (1972) for the Second Gondwana Symposium, and hence full documentation here seems unnecessary.

As I pointed out some years ago (1966) Triassic faunas may be roughly divided into three successive groups, (A) early, (B) intermediate, and (C) late, although it is obvious that such distinctions cannot be completely clear-cut, and transitional assemblages may be expected. A-type faunas have long been known from the Upper Beaufort beds of South Africa, containing mainly therapsids, although with early members of other groups, notably thecodonts. C-type faunas are almost ubiquitous, being known from redbeds Late Triassic deposits in Europe, North America, South Africa, China, and (now) South America. In such faunas dinosaurs are already prominent, and their thecodont predecessors are still present, whereas therapsids are practically extinct (although the earliest mammals descended from them have now appeared).

As to B-type faunas, these were until recently almost entirely unknown, since deposits of Middle Triassic age in the northern continents are mainly marine, and in South Africa the Molteno beds, of Middle Triassic age, appear to be nearly barren of fossils (although footprints are abundant). What should one have expected in B-type faunas? Obviously, a transition between

A and C, with a gradual reduction of therapsids and an increase in archosaurs, including a variety of thecodonts and the beginnings of the dinosaurs. The B-type faunas now known from the southern continents do show these expected transitional features. But, in addition, they show positive characteristics of their own, in the great flourishing of gomphodont cynodonts and rhynchosaurs — groups that had their beginnings in the A-type faunas of the Early Triassic but seemed of little importance.

Let us first consider the South American situation. A-type faunas are certainly present in the Puesto Viejo Formation and not improbably in the Cacheuta series, as Bonaparte believes (although the evidence is still scanty). The C-type is present both in the upper part of the Los Colorados Formation, as now being developed by Bonaparte, and in the El Tranquilo Formation. Between, we have in Argentina the succession Chañares-Los Rastros-Ischigualasto, three formations that lie conformably one above the other in the Talampaya basin. The Los Rastros beds are almost barren of fossils, but it is, I think, generally agreed that the Santa Maria Formation of Brazil is equivalent, and thus, for vertebrates, our sequence may read Chañares-Santa Maria-Ischigualasto. All three clearly include B-type reptile faunas.

The Chañares beds, earliest of the three, clearly are an early part of the B complex. The gomphodonts are members of the traversodontid family, and the diademodontids and trirachodontid types present in the Scythian *Cynognathus* beds of South Africa appear to be extinct. The carnivorous cynodonts are of relatively advanced types — rather more advanced than *Cynognathus.* Rhynchosaurs are absent, but this, as noted above, appears to be due to some ecological factor, since primitive rhynchosaurs were already present in the A-type *Cynognathus* zone. And, while few thecodonts were present in the *Cynognathus* zone, they are here already varied in nature and in some cases at least, of a progressive type.

The Santa Maria beds are quite surely later in age than the Chañares beds but, just as the presumably equivalent Los Rastros beds lie in the break above the Chañares, the fauna of the Santa Maria beds follows that of the Chañares with some advances but without any major change. Among the dicynodonts, *Dinodontosaurus* continues little changed into the Santa Maria. Of gomphodonts, the Santa Maria *Traversodon,* although poorly known, may well be descended with little change from *Massetognathus.* The Santa Maria carnivorous cynodont *Belesodon* appears to be but an enlarged edition of *Probelesodon* of the Chañares. In both Chañares and Santa Maria beds, most of the thecodonts are imperfectly known, but it is very probable that, given more adequate material, several close comparisons may come to be made, and *Cerritosaurus* of Santa Maria is very similar structurally to *Chanaresuchus* of the earlier formation. As Cox (1968) states, "the Chañares fauna is only slightly earlier than that of the Santa Maria." The only advance of any note is that here (as might be expected) we have the first sign of the evolution of dinosaurs from thecodonts in *Staurikosaurus* Colbert and possibly the fragmentary materials described by Huene as *Spondylosoma.*

Next above the Los Rastros Formation, without disconformity, lies the Ischigualasto Formation, from which a very considerable fauna is now known. The only dicynodont, *Ischigualastia,* is a large form of no particular stratigraphic significance. Gomphodonts of several genera — *Exaeretodon, Proexaeretodon, Ischignathus* — are exceedingly abundant, especially in the upper part of the formation. All are traversodonts that are more advanced than those of the Chañares and Santa Maria beds. Carnivorous cynodonts are rare and represented only by fragmentary remains that have been referred to the Santa Maria genus *Chiniquodon.* Thecodonts are, again, fairly common and varied. *Saurosuchus* is a relative of *Luperosuchus* of the Chañares but of larger size; *Proterochampsa* is similarly a large member of the *Chanaresuchus-Cerritosaurus* group. *Triassolestes,* originally thought to be a dinosaur, is probably a thecodont, but perhaps a crocodiloid relative. Interesting is the presence of *Aetosauroides,* first representative of a thecodont type that was to continue, apparently little changed, to Late Triassic times. Of dinosaurs we now have (although as rarities) the probable saurischians *Herrerasaurus* and *Ischisaurus* and, most interestingly, the oldest known ornithischian, *Pisanosaurus.* Despite advances, we have a close tie with the Santa Maria in that the common Ischigualasto rhynchosaur *Scaphonyx* (thoroughly studied in an unpublished thesis by Sill) is almost indistinguishable from the species present in the Santa Maria. Chatterjee (1969) has suggested that the Santa Maria localities containing *Scaphonyx* are later than those containing the remainder of the fauna. But there is no geological evidence to support this suggestion; all the vertebrate fossils, rhynchosaurs, dicynodonts and others, appear to come from the relatively thin upper portion of the Santa Maria Formation. In sum, the fauna of the Ischigualasto Formation is advanced over that of the Santa Maria, but the difference is not great, as Bonaparte has noted.

We lack any means of correlation of these South American beds with the standard marine series, but since these faunas are obviously post-Scythian and pre-Norian, it is natural to suggest a one-to-one correlation of Chañares-Santa Maria-Ischigualsto with Anisian-Ladinian-Carnian. I have in the past expressed doubts as to whether the horizon of the Ischigualasto Formation was as high as the Carnian. In the European Keuper reptile remains are known only from the upper, Norian, part of the sequence and we have no knowledge of the reptile fauna of Carnian times. Further, in the Ischigualasto Valley the Los Colorados redbeds tower for some 400–500 meters above the top of the Ischigualasto beds and, except for a single dicynodont, our knowledge of the Los Colorados fauna is derived from the very topmost beds of this formation, so that it is possible that the lower part of these beds are of Carnian age. However, consideration of the faunas found in India and the northern continents (discussed below) suggests that our B-type faunas continued into Carnian days. It is thus very likely that the age of our B-type Middle Triassic faunas conflicts with the classic division of the Triassic into lower, middle and upper. Stratigraphically the Middle Triassic includes Anisian and Ladinian, while the Upper Triassic includes Carnian, Norian and Rhaetic; as regards vertebrates it is probable that the Middle Triassic includes Carnian and Anisian and Ladinian as well, with the "upper" C-type faunas restricted to the Norian and Rhaetic.

If one wishes to compare the Chañares and other South American B-type faunas with those of other continents, one naturally turns first to South Africa, since current theories of continental drift suggest that in the Triassic South America and Africa were closely apposed to one another. If this was the case one would expect similarities between the faunas of the two continents. But even if the South Atlantic were then nonexistant, there would remain a considerable distance between the Talampaya basin, and even the Santa Maria region, and the fossiliferous beds of east and south Africa. One should expect that there might be a considerable difference between the reptile faunas of these regions just as there is today a very considerable difference between the reptile faunas of, for example, California and the Atlantic coast areas of North America.

The African beds concerned are (1) the Molteno beds of the

Stormberg Series of South Africa, (2) the Ntawere beds of Zambia, and (3) the east African Manda beds.

The Molteno beds are quite surely Middle Triassic in age and should contain a fauna of the B-type. But while footprints are tantalizingly abundant, actual fossils are rare, and such few as have been described are of uncertain stratigraphic position and may either come from the top of the *Cynognathus* zone (as in the case of a cynognathid) or from the base of the redbeds (as in the case of a traversodont gomphodont).

The Ntawere beds are as yet not fully explored and as yet little material has been described (*cf.* Cox, 1969). Two zones appear to be present. The lower, in which *Diademodon* is present, may well be equivalent to the upper part of the *Cynognathus* zone, with an A-type fauna. The upper zone fauna includes two dicynodonts — the stahleckeriid *Zambiasaurus* and the kannemeyeriid *Sangusaurus,* two traversodont cynodonts, *Luangwa* and a second form as yet undescribed, and fragments of thecodonts. In default of fuller data, the age of this fauna is difficult to determine. The presence of traversodonts suggests the B-type; but traversodonts occur at an Early Triassic age in Argentina and may well have been as early in appearance in Africa.

Of especial interest is the Manda Formation of east Africa, from which a very considerable fauna is known, owing to collections made for Huene, by Parrington, and by an English expedition a decade ago. Unfortunately much of the known material is undescribed or described in only preliminary fashion. I am indebted to A. J. Charig for the faunal list given here. There are three dicynodonts, *Kannemeyeria, Tetragonias,* and a third undescribed form. No carnivorous cynodonts are as yet described, but gomphodonts are numerous and varied, including the diademodontids *Theropsodon* and (?)*Aleodon,* the trirachodontid *Cricodon* and a variety of traversodontids of which the only remains as yet described are assigned to four species of the genus *Scalenodon.* Some seven thecodonts have received names, including the prestosuchids *Mandasuchus* and (?)*Stagnosuchus,* and five further genera not assigned to families — *Parringtonia, Teleocrater, Hypselorhachis, Nyasasaurus* and *Pallisteria.* The abundant rhynchosaur remains pertain to the primitive genus *Stenaulorhynchus.*

The abundance of gomphodonts and rhynchosaurs indicates that we are dealing with a typical B-type fauna, and the presence of *Kannemeyeria* and of diademodontid and trirachodontid gomphodonts suggests a relatively early age. The fauna is obviously earlier than that found at Ischigualasto, and the Santa Maria and Chañares faunas are the two South American assemblages with which comparisons might reasonably be made. On the whole, it is the Chañares fauna that seems to be the closest. The absence of rhynchosaurs in the Chañares beds removes one basis of comparison which might have been hoped for. Not improbably some of the Manda thecodonts will show affinities to Chañares genera when fully described. Crompton tells me that some of the Manda gomphodont specimens are closely comparable to *Massetognathus,* but here again we must await further publication. It is not unreasonable to expect that when the Manda fauna is fully described it will prove to be rather similar to that of the Chañares, but of a somewhat earlier date.

In more northern regions — India, Scotland and Nova Scotia — are assemblages that contain characteristic elements of the B-type fauna but are usually considered as of Late Triassic age. In the Maleri beds of India only three named tetrapods are present. These are: (1) a stereospondylous labyrinthodont generically identical with *Metoposaurus,* common in the Upper Triassic of both Europe and North America but otherwise unknown in presumed "Gondwana" areas; (2) a phytosaur, difficult to assign to a given genus (the systematics of phytosaurs are in a confused state) but representing a group unknown elsewhere in "Gondwana" areas except in Morocco; (3) a rhynchosaur *Parasuchus* [*Paradapedon*] of an advanced type which Chatterjee believes related to *Scaphonyx* of South America and *Hyperodapedon* of Elgin. The presence of a metoposaur and phytosaur in a supposed Gondwana region presents an interesting geologic problem, but the question of the age of the Maleri is almost equally interesting.

The Maleri is considered to be "Upper" Triassic; but while "upper" in a stratigraphic sense, it may well represent a Carnian fauna of our B-type. As regards phytosaurs, they are unknown in Europe before the Norian, but this group obviously had a long antecedent history (disregarding the question of the age of *Mesorhinus*). Metoposaurs, again, are "Upper" Triassic, but it is not improbable that there may have been older antecedent stages in the development of these peculiar stereospondylous labyrinthodonts.

Rhynchosaurs, in the form of the advanced genus *Hyperodapedon,* are present in the Elgin beds of Scotland, which Walker (1961) believes to be of Norian age. His conclusions may be correct, and this may mean a late survival of rhynchosaurs in Europe. But it must be pointed out that there is no trace of a rhynchosaur in the Norian Keuper of continental Europe, and hence it may be suggested that the Elgin beds are pre-Norian, perhaps Carnian in age. The Elgin fauna is a sparse one; there is nothing to represent the typical dinosaur fauna of the continental Norian (the systematic position of *Ornithosuchus* is questionable). Walker's correlation with the Norian is based mainly on the presence of *Stagonolepis,* a close relative of *Aetosaurus* of the continent. But we now know that the aetosaurid pattern was already present in the Ischigualasto beds in the form of *Aetosauroides* [*Argentinosuchus*], which is still incompletely known but appears to be a fully developed member of this group.

Most interesting is the report by Baird (1962 and *in litteris*) of the presence in beds in Nova Scotia which have been correlated with the Newark series of the Atlantic seaboard of the United States, of both of the most characteristic elements of the B-type fauna — rhynchosaurs and a gomphodont jaw! The Newark is a characteristically C-type series, as witnessed not so much by the rare dinosaurian fossil remains as by the vast numbers of dinosaur footprints. Are we dealing in these Nova Scotia finds with a very late survival of gomphodonts and rhynchosaurs? Or — more probably, I think — these supposed Newark equivalents in Nova Scotia may, in their lower beds, extend downward from Norian to Carnian age, into the time of existence of the B-faunas. Parenthetically, while the familiar red Triassic deposits of the western United States — Chinle, Dockum, Popo Agie — are usually considered as of quite Late Triassic age, we find in them mainly metoposaurid amphibians and phytosaurs, and little representation of the abundant dinosaurs found in the European Norian, the redbeds of South Africa, the Late Triassic of China and, apparently, in the Newark series proper. Is the nature of the faunas of these western beds associated with ecological factors or are they of pre-Norian age?

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ECOLOGY, SELECTION AND SYSTEMATICS

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Abstract. Three different kinds of ecological relationships between newly separated species are examined, with the aim of establishing their expected effects on the systematic differences between the species involved. In cases of slight difference between the habitats of two products of recent speciation, selection can be expected to favor specific competitive mechanisms, but taxonomic differences would be expected to be slight, and examples of hybrid superiority would be common. Where the habitats of the two species are markedly different, as along a steep ecological gradient, adaptation to the different places will result in species that become broadly overlapping in habitat, and taxonomically different in many clearly adaptive characters. Although this latter process leads to species with somewhat different food habits, it would not lead to food specialization, even if the two species were originally limited in abundance by food and in competition for it. True food specialization, in the form of monophagy, is most likely to evolve in the presence of a superabundance of several kinds of food, owing to increased efficiency of handling, digestion and metabolism, and is improbable among species in competition for food. Closely related monophagous species should differ markedly in a few characters, and hybrids should be inferior. Examples of the three situations are described, plethodontid salamanders being used for the first two and leaf-mining insects for the third.

Introduction

Classically, the relationship between systematics and ecology has been approached by first taking systematics as the exploration of genomic diversity, and then turning to ecology for explanations that were secondary to the origin of differences. This approach is epitomized by the recent comment to me that the reproductively isolated entities within *Paramecium aurelia* could

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now be considered species because their isoenzyme patterns are visibly different. Such a viewpoint surely gets the classification much too far away from the biology. As an antidote, I propose to examine the relationship from the standpoint that ecology provides the set of opportunities that can be exploited by diversification of the genome. The approach is not original, as it is the basis for the idea of adaptive radiation, but the impact of ecology on systematics deserves reexamination. In this, we should separate the passive background from the active; that is, those factors that set the conditions, and those that are able and likely to respond by evolving themselves. These two classes, unfortunately, will not remain constant for us. For example, it would be agreed that the distinction between nonliving and living parts of the environment might provide such a preliminary classification, but as far as I can discover, this is not the case. The distinction between the vegetation on one hand and the climate and substrate on the other is clear enough. The physical gradients provide the passive background, making physiological demands on a potential additional plant species, and the various competing species of plants provide the active counteradapting background, making ecological demands.

However, when we consider the active and passive background of animals, particularly carnivorous ones, the distinction between plants and the physical environment becomes less important than the distinction between both of those on the one hand and other animals on the other. Indeed, there are few cases of terrestrial predators which are distributed concordantly with even the dominant plants, and when this coincidence does occur, the plants are used in a nonliving context, as when they are required for nest sites.

This example provides the opportunity to emphasize the distinction between selection for physiological adaptation and selection in response to the ecological pressures of competition and predation. It is to the latter to which I wish to address myself principally, but I first give an example of the simultaneous operation of both. This will be followed by a description of what seems to me to be an unusual opportunity to investigate the ecological interaction between one species and several geographically varying populations of another, closely related one. From that, I hope to be able to generalize some about a fruitful investigation of other kinds of systematic consequences of ecological phenomena.

An Analysis of the Exploitation of a Undimensional Gradient

As has been emphasized by Dunn (1926), (Hairston, 1949), Organ (1961) and others, the evolution of the Dusky Salamanders of the genera *Desmognathus* and *Leurognathus* is describable in terms of adaptation to a linear series of habitats from aquatic to terrestrial.

This unidimensional array of pertinent physical environments facilitates the analysis of each species' most immediate biological environment: namely, its closest relatives.

My own early analysis showed that the coexistence of five species was possible, when they used the entire physical gradient from completely aquatic to terrestrial. The species involved are *Leurognathus marmorata, Desmognathus quadramaculatus, D. monticola, D. ochrophaeus* and *D. wrighti.* The distribution of the four species of *Desmognathus* is shown in Figure 1. With no further information, however, it was not possible to determine whether more species could be accommodated in this presumably competitive series.

Some years later, Organ was able to provide a tentatively negative answer when he investigated the ecological distribution of the same four species of *Desmognathus* in an area where a fifth species, *D. fuscus,* was found. He found that at nearly every location, the maximum number of species present was four. *D. fuscus* could coexist either with *D. quadramaculatus* at high elevations or with *D. monticola* away from large streams at lower elevations but not with both.

Thus, the limit imposed by the presumably competitive relationships seems to have been reasonably well estabilshed, but a more detailed look at the data suggests that steepening of the moisture gradient may reduce the number of species that can be accommodated from the competitive standpoint. At high elevations, atmospheric moisture, however expressed, is as great far from water as it is over a stream at low elevations (Hairston, 1949). This correlates very well with the combined vertical and horizontal distributions of the two most terrestrial salamanders, *Desmognathus ochrophaeus* and *D. wrighti. D. ochrophaeus* is confined to a zone near streams at low elevations, none having been found more than 15 feet from a stream at elevations below 3000′, but its distribution is unrelated to surface water above 4500 feet. *D. wrighti,* with its distribution unrelated to water in summer, apparently cannot compete with its congeners close

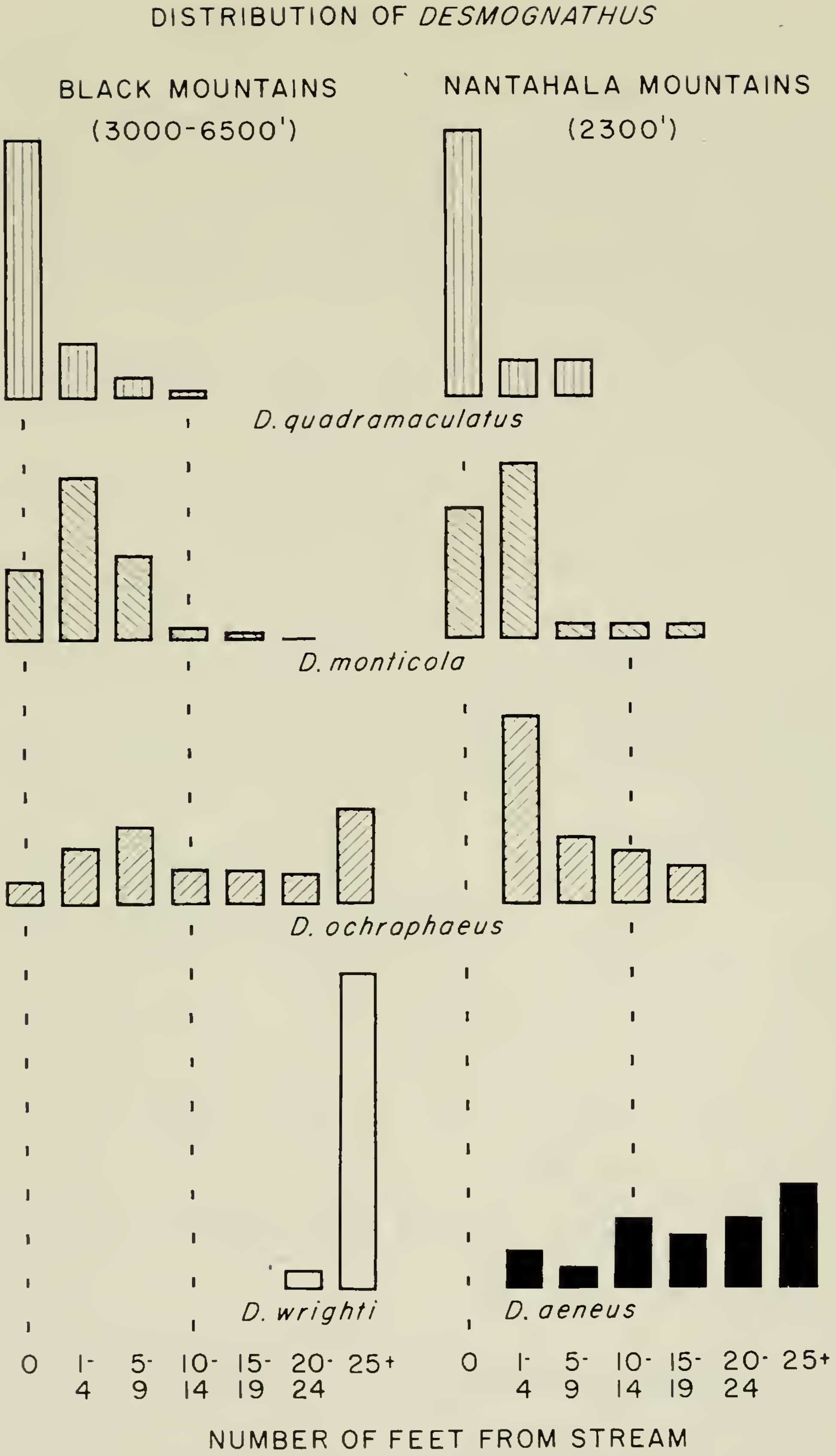

Figure 1. The ecological distribution of the species of the salamander genus *Desmognathus* in two different mountain ranges in North Carolina.

to streams at low elevations, and cannot persist away from streams there because of the lower moisture.

It is therefore with some interest that one notes the coexistence of four species of *Desmognathus* at low elevations (down to 2200 feet) in the Nantahala Mountains. *D. wrighti* does not occur at low elevations, but a study of the ecological distribution of the genus shows the presence of a terrestrial species, *D. aeneus*. This species, which is the size of *D. wrighti,* but more slender, was found closer to streams than *wrighti* usually is in summer, but clearly occupies the same general position at the terrestrial end of the environmental gradient (Fig. 1). It seems anomalous that it should be present, although *D. wrighti* is unable to occupy the corresponding habitat at low elevations near its range. It was postulated above that this inability is related to reduced moisture at low elevations. This suggests that there may be a climatic variation that permits the existence of a low-altitude terrestrial *Desmognathus* in the Nantahala Mountains. An examination of rainfall records reveals that such is the case. In the Coweeta Experimental Forest, the location of the distributional study, the average annual rainfall ranges from 75 inches at 2240 feet to 93 inches at 3870 feet. This is appreciably higher than the rainfall at comparable elevations elsewhere in the Southern Appalachians. For example, at the foot of the Great Smoky Mountains, Bryson City, N.C. has an average annual rainfall of 52.12 inches. At the foot of the Black Mountains, Montreat and North Fork have 53.61 and 51.78 inches respectively, and between the Smokies and the Blacks, the French Broad Valley receives from 38.45 inches at Enka to 47.61 at the Asheville-Hendersonville Airport.

Among other locations at comparable elevations in the Southern Appalachians, only the region from Brevard to Highlands, N.C. receives as much rain as the general area south and west of the Little Tennessee River. Comparable rainfall is found elsewhere only at high elevations (71.20 inches at Mt. Mitchell, 6684′ in the Black Mountains, and 81.71 inches at Clingman's Dome, 6643′ in the Great Smoky Mountains).

The end of the series of species seems to be determined by climate, with high rainfall permitting the addition of a small terrestrial species. On larger and higher mountains, when the tops are (or once were) covered with conifer forests and rainfall is high, the terrestrial species is *Desmognathus wrighti,* which is confined to elevations above 3500 feet; in that part of the mountains where the rainfall is high, even at low elevations, *Des-*

mognathus aeneus occupies the terrestrial end of the series. In other areas, the series stops with the third species, *D. ochrophaeus.* It does not appear possible for another species to enter the series in the midle, as shown by the situation with *D. fuscus* at White Top Mountain in Virginia. Competition thus seems to determine how similar any pair of species can be and still coexist. When the climate would require the next most terrestrial species to overlap the habitat of *D. ochrophaeus* to too great an extent, only three species are found.

This situation seems to present an unusually clear example of the evolutionary exploitation of a simple environmental gradient and of the limits of this diversifying exploitation that are set by competitive interactions. The limits to "species packing" are demonstrated as clearly as post-facto analysis could permit.

Moreover, it provides a miniature model for the early stages in the evolution and diversification of the family Plethodontidae.

POST-SPECIATIONAL EVENTS: INCREASED COMPETITION OR COEXISTENCE?

The kind of analysis made in the preceding section differs from large numbers of published descriptions only in being a little more tidy than most. If the field is to progress, such statements will become the beginning of studies at the interface of ecology and systematics, rather than representing final conclusions. The choice among investigations of ecological distribution should depend upon the respective opportunities that they present for experimental tests of hypotheses of systematic status or ecological processes. One of the points which I wish to make most strongly is that experimentation related to ecological interactions can yield important information about evolutionary events, provided that care is taken to select appropriately favorable situations for study. One such situation that seems to be especially suitable for field manipulations is represented by two species of *Plethodon,* an exclusively terrestrial genus of salamanders. The location is also the Southern Appalachians.

Plethodon jordani is endemic to the southern Appalachians. Through much of its range, it is confined to higher elevations, resulting in a fragmented distribution consisting of a number of isolated populations, many of which are morphologically distinct from each other. These populations have been studied repeatedly, and have been classified as belonging to as many as four distinct species (Grobman, 1944). Whenever specimens have been taken from intermediate locations, they are intermediate in color between the adjacent different populations. This discovery led to the eventual inclusion of all of these populations within *Plethodon jordani* and the recognition of seven subspecies (Hairston and Pope, 1948; Hairston, 1950). The subspecies are no longer recognized, largely because at least some of the color characters are distributed independently of one another. The situation as it is presently known is described by Highton (1970, 1971) and by Highton and Henry (1970), who add the electrophoretic patterns of plasmaproteins to the characters for which distributional data are available.

Plethodon glutinosus is widespread throughout the eastern United States. In the Southern Appalachians, it tends to occur at lower elevations than those at which *P. jordani* does, and I have suggested that the sharp altitudinal replacement of the two species is the result of competitive exclusion (Hairston, 1949, 1951). Although easily recognizable color differences are known for at least four geographically distinct parts of the *P. glutinosus* population (Highton, 1962, 1970, 1971), the population in the area discussed herein consists of only one of these. *P. glutinosus* is thus morphologically more uniform than is *P. jordani.* The above-mentioned altitudinal separation of the two species is not the case everywhere, however. Over the southeastern part of the range of *P. jordani,* the two species occur together over nearly the entire range of altitudes available, indicating that competition does not play a significant role in their distributions. This observation, reported by me for a few vertical transects (Hairston, 1951) has been confirmed and extended by Highton. The fact that in this area *P. jordani* occurs at lower elevations and *P. glutinosus* at higher elevations than elsewhere strengthens the conclusion that in the areas of altitudinal replacement, there is intense competition in the narrow vertical zones of overlap. It is this geographical difference in ecological relationship between the two species that provides an unusual opportunity to investigate the phenomenon of competition in the field, and to obtain evidence on the sequence of evolutionary events accompanying competitive interactions between two similar species.

The above account is oversimplified from the taxonomic standpoint. Over most of the area west of the French Broad River, the two species are distinct, but Highton has found hybrids at appropriate elevations on some of the mountains, and intergradation is so extensive in the Nantahala Mountains that the local form of *P. jordani* was once described as a subspecies of *P.*

glutinosus (Bishop, 1941). Highton has called specimens from intermediate elevations a hybrid swarm. Two detailed vertical transects in the Southeastern Nantahalas at Coweeta Experimental Forest show that simple explanations of the relationship are unlikely to be satisfactory. The forest has two more or less parallel roads that ascend to the top of the mountain. The roads diverge slowly from the foot of the mountain at 2200 feet, being a little more than one mile apart at 3200 feet and around two miles apart at the points where they reach the top of the ridge at 4100 and 4500 feet, respectively. In October, 1971, a transect was carried out along the more northern road, to be referred to as the Shope Creek Road. The conventional expectation would be of continuously increasing similarity to *P. jordani* and decreasing similarity to *P. glutinosus* with increasing altitude. The comparison was made on the basis of color alone, no other known character being of value in that part of the range. Four different color characters are possible. *P. jordani* is characterized by red legs and a pale belly; *P. glutinosus* has extensive white spotting, especially on the sides, and a black belly. A population of *P. jordani* 10–15 miles to the east has extensive brassy spotting on the back, as well as some white spotting on the sides, but at present seems to be distributed discontinuously from the Nantahala population. A few specimens from the transect had brassy spots, but were too few to yield meaningful information. Arbitrary scales were established to compare the relative amount of red on the legs, white spotting, and darkness of belly color. Six to 20 specimens were collected at each of 11 elevations from 2200 to 4300 feet. For each collection, an average intensity of each character was established by five different observers, and the results pooled. The three characters changed in exactly the same way along the transect. The results for two of them are shown in Figure 2. The reversal of the expected trend led to a transect of the southern road (Ball Creek) in 1972. The results, shown in Figure 3, conform to the original expectation, but do not agree with the Shope Road transect, which was repeated in 1972 with virtually identical results to those obtained in 1971 (Fig. 2).

Although the 3800-foot site is located on an east-west ridge, the same is true of all higher sites, and no obvious vegetational differences could be seen to account for the difference between the transects — impressions confirmed in the records from 69 widely dispersed rain gauges (Dils, 1957).

Whatever the eventual explanation for these anomalous data,

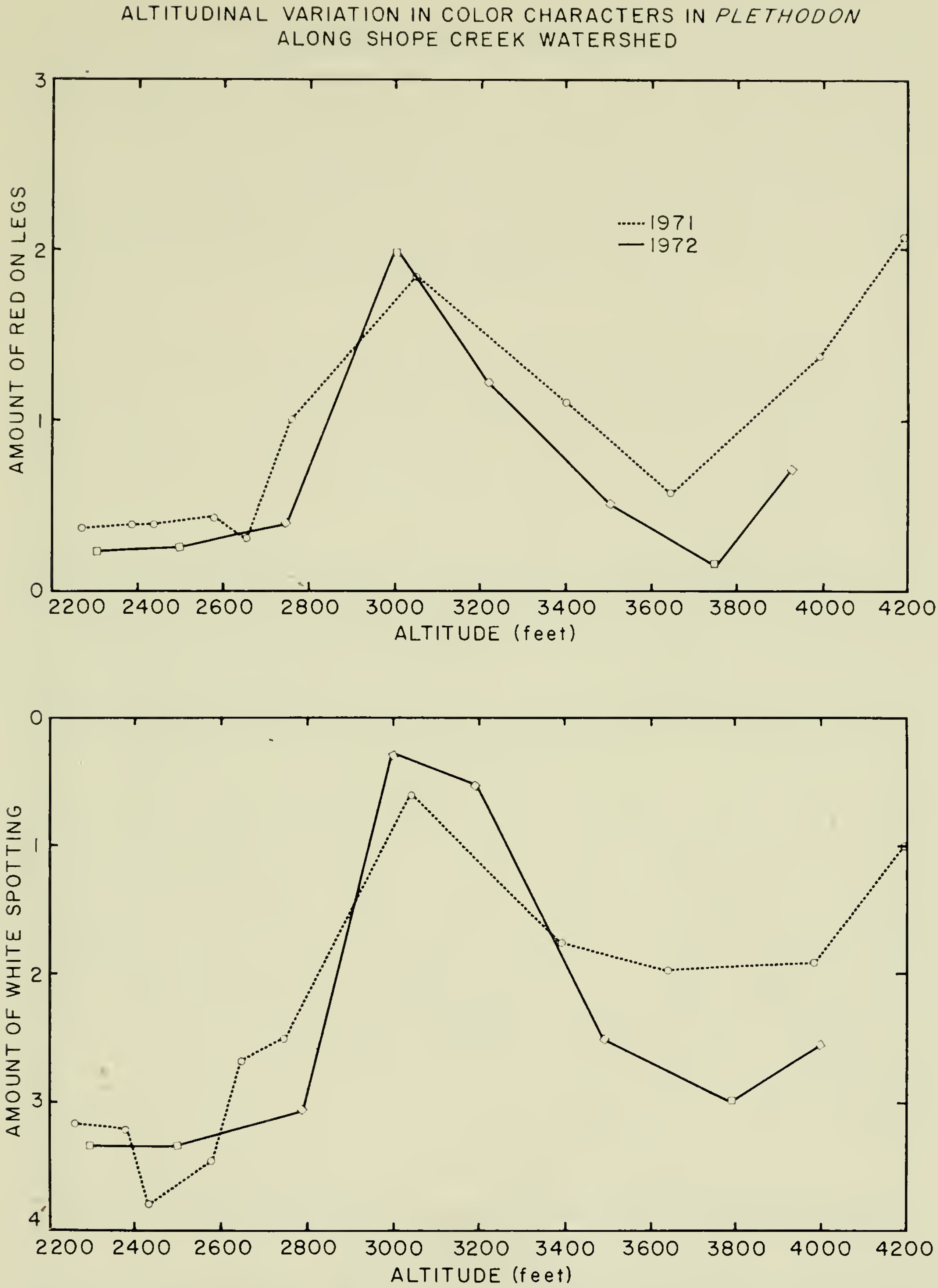

Figure 2. The vertical distribution of two color characters in the salamander genus *Plethodon* along the Shope Creek transect in the Nantahala Mountains in North Carolina. The scale for white spotting has been inverted because white spots are characteristic of the low-altitude species.

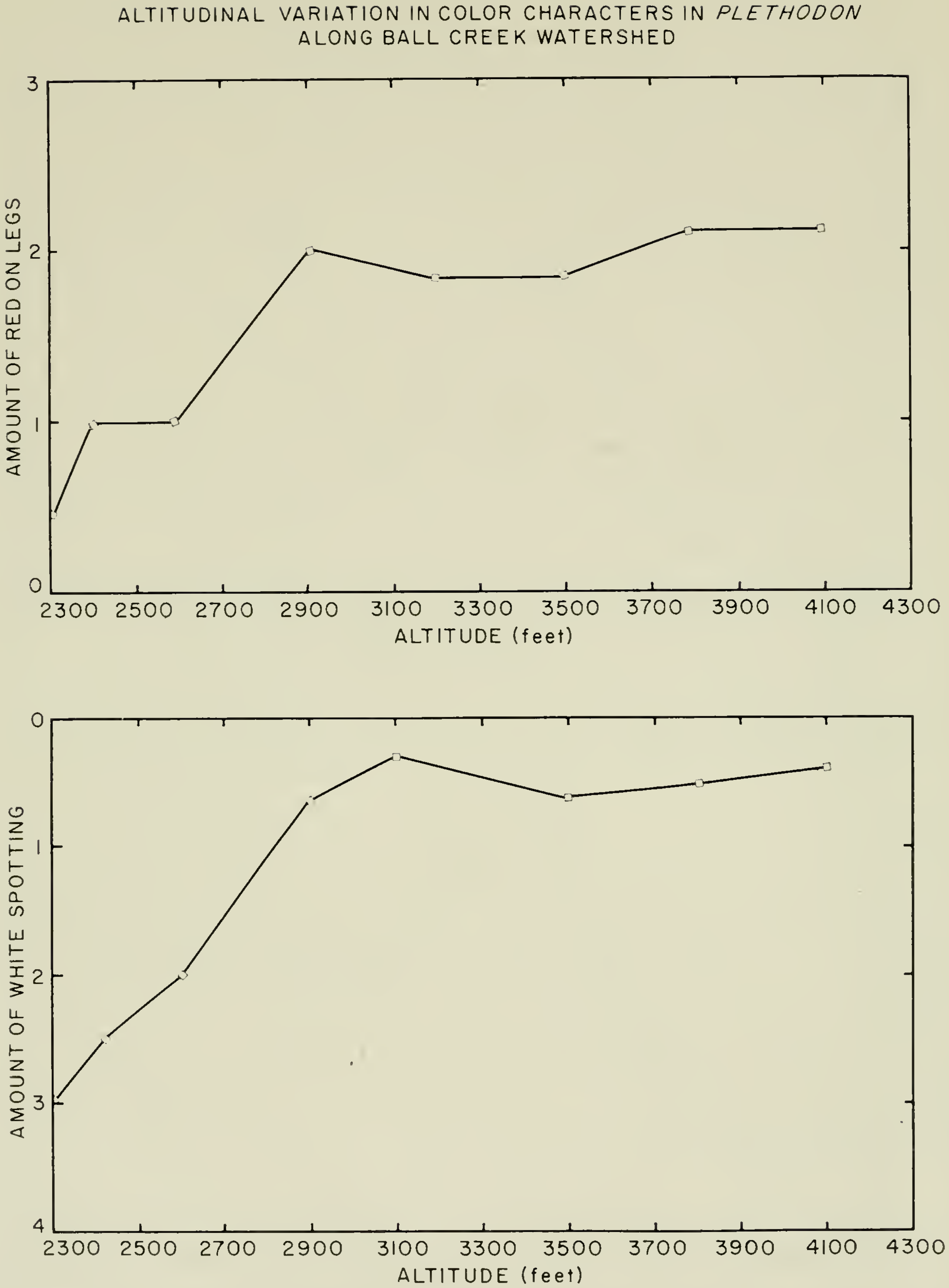

Figure 3. The vertical distribution of two color characters in *Plethodon* along the Ball Creek transect, for comparison with Figure 2.

they reflect complications in the relationship between the two species, and further investigations may reveal or at least suggest very local selective forces.

The situation in the Nantahalas gives a strong indication of close taxonomic relationship between *P. glutinosus* and *P. jordani,* and is thus useful information in suggesting ecological and especially evolutionary questions about the two species elsewhere in the Southern Appalachians where hybridization is absent or very rare.

Current evolutionary theory would explain the observed ecological distributions in these other areas in the following manner: assuming, as seems likely, that *Plethodon glutinosus* and *P. jordani* share a common ancestor in the not very remote past, the speciational event separating them left two species with adjacent geographical ranges and very similar ecological requirements. *Plethodon jordani* presumably occupied the southern part of the Blue Ridge physiographic province, and the relevant part of *P. glutinosus* occupied the adjacent part of the Piedmont province. With a warming climate, *glutinosus* has invaded the valleys of the Blue Ridge province, but competition from *jordani* has prevented *glutinosus* from extending its range to the tops of at least some of the mountains, notably the Great Smoky Mountains, the Black Mountains, and the Unicoi Mountains. Throughout most of the rest of the area of common distribution, one or both species have evolved into ecologically divergent directions, with the result that competitive exclusion no longer operates, and the two species coexist over a wide range of elevations. This situation would represent character displacement in the use of some ecological requirement as yet unidentified. In the areas of competitive exclusion, the vertical overlap of 200 feet represents the uncertainty of outcome of competition owing to climatic variability, *P. jordani* being favored by cool, wet years and *P. glutinosus* by the reverse conditions.

Thus, in conventional theory and as far as numerous observations have revealed, we have the same two species coexisting in some areas and in intense competition in others. Geographic variation in color of *P. jordani* provides independent identification of representatives from the two ecologically different populations, and this and other features make it feasible to undertake experimental manipulations to test the accuracy of the interpretations that I and others have made of the present distributions of the local populations of the two species. This should be done by reciprocal removal experiments and by exchanging numbers of *Plethodon jordani* between the two areas of presumably different ecological relationships. Inasmuch as they differ in color pattern, the introduced individuals and their descendents would be readily identifiable for an indefinite number of years after the start of the experiments.

The most obvious first test of the interpretations would be to remove each species separately from different plots in the different areas where competition is and is not expected. If the interpretation is correct, the remaining species should show a much greater response in the area of narrow vertical overlap than in the area of wide vertical overlap.

Whatever the outcome of these simple removal experiments, they would help resolve an implicit contradiction in ecological theory. This is the conflict between the often used theory that distributional overlap between closely related species implies an appreciable amount of competition (Levins, 1968; MacArthur, 1968) and the converse that the same overlap implies that competition is reduced or absent (Crombie, 1947; Hairston, 1951; Brown and Wilson, 1956; MacArthur, 1972: 29 ff). This conflict is rarely stated overtly, but its resolution could have a profound effect on ecological theory, including much that has been written about niche breadths and community matrices.

The implications of the simple removal experiments are more directly ecological than they are evolutionary. The combination of ecological and systematic situations provides the opportunity for more sophisticated experiments whose results could yield important insights into the recent influence of natural selection on the direction of evolution in the several populations of *Plethodon jordani*. These experiments would consist of reciprocal transplants of populations of *P. jordani* between an area of narrow overlap and one of wide overlap. The subsequent changes in the transplanted *jordani* populations and in the *P. glutinosus* populations newly exposed to the foreign *jordani* would reveal the direction of recent evolution with respect to interspecific competition.

If *P. jordani* from the area of wide overlap survived in the area of narrow overlap, and the *P. glutinosus* population increased, the interpretation would be that in the area of wide overlap, *P. jordani* has evolved so as to decrease its competitive interaction with *glutinosus*. If *P. glutinosus* has evolved in the same way, the reciprocal experiment should result in no change in the *glutinosus* population, and it might result in an increase in the *jordani* population introduced from the area of narrow overlap, because the *jordani* would not be meeting as much competition as it had been experiencing before the experiment.

Conversely, if the *P. jordani* transplanted from the area of narrow overlap increases in the area of wide overlap at the expense of the local *P. glutinosus,* it would be necessary to conclude that recent evolutionary history had produced a specialization in *jordani* for some specific competitive mechanism.

A decrease in and eventual disappearance of *jordani* moved from the area of wide overlap, combined with an increase in the local *glutinosus,* would be interpreted to mean the evolution of a specific competitive mechanism in that population of *glutinosus.*

The complete set of possible experimental outcomes and their interpretations is given in Tables 1 and 2. Specifically omitted from the tables are the highly necessary controls. For the removal experiments, the only controls required are undisturbed plots containing both species. The reciprocal transplantation of populations of *P. jordani* will require elaborate controls. First, one must be satisfied that the salamanders can be moved at all and continue to thrive. This will require transplanting animals within an area where their ecological relationships appear to be constant. Assuming the success of such an experiment, it will also be necessary to provide assurance that they are physiologically capable of existing in the remote area where the competitive relations are presumably different. For this control, it will be necessary to first remove both species from a plot and then introduce the foreign *jordani.* Its survival would assure an interesting result on those plots where it was introduced into contact with *glutinosus.* The failure of any of these controls would of course mean that the main experiment in reciprocal transplantation of populations was a failure. This is a gamble taken by anyone planning a controlled experiment.

If the controls succeed, the experiment should permit one to choose with confidence between the following hypotheses: First, that after speciation natural selection has favored ecological diversification with resultingly greatly lowered competition and a greatly increased area of coexistence; and second, that after speciation and reinvasion, natural selection has favored the development in at least one species of mechanisms to increase its competitive ability and thus exclude the congener from all or nearly all of its range. The ability to choose between the two hypotheses would greatly advance our ability to interpret systematic-distributional data from a large array of situations where *post facto* conclusions are all that can be expected.

TABLE 1. The plan and possible outcomes with their interpretations of experimentation in the area where *Plethodon jordani* and *P. glutinosus* overlap broadly in vertical distribution. All controls are described in the text.

MANIPULATIONS		OUTCOME	INTERPRETATION
A. Remove *jordani.*	1. Replace with *jordani* from area of narrow overlap.	a. Disappearance of moved *jordani.*	Local *glutinosus* has a competitive adaptation to foreign *jordani* and local *jordani* has evolved ecological character displacement.
		b. Persistence of moved *jordani.*	(I) Combined with a decrease in abundance of *glutinosus,* means that introduced *jordani* had evolved a specific competitive mechanism against *glutinosus.*
			(II) Combined with constant *glutinosus* population, means that local *glutinosus* has evolved ecological character displacement.
	2. Leave local *glutinosus* alone.	a. No change in abundance of *glutinosus.*	Means that there was no competition with *jordani.*
		b. Increase in abundance of *glutinosus.*	Means that there was some competition at a low level.
B. Remove *glutinosus.*	1. Leave local *jordani* alone.	a. No change in abundance of *jordani.*	Means that there was no competition with *glutinosus.* (Reciprocal of A 2 a)
		b. Increase in abundance of *jordani.*	Means that there was some competition with *glutinosus* at a low level. (Reciprocal of A 2 b)

TABLE 2. The plan and possible outcomes with their interpretations of experimentation in the area where *Plethodon jordani* and *P. glutinosus* have a narrow zone of vertical overlap. All controls are described in the text.

MANIPULATIONS		OUTCOME	INTERPRETATION
A. Remove *jordani.*	1. Replace with *jordani* from area of wide overlap.	a. Disappearance of moved *jordani.*	Local *glutinosus* has a specific competitive adaptation to all *jordani; glutinosus* should increase in abundance.
		b. Persistence of moved *jordani.*	(I) If *glutinosus* increases in abundance or remains stable, indicates that introduced *jordani* has evolved ecological character displacement with respect to all *glutinosus.*
			(II) If *glutinosus* decreases, indicates specific adaptation by area I *glutinosus* to coexist with all *jordani;* especially strong if combined with A 1 b (II) of Table 1.
	2. Leave local *glutinosus* alone.	a. No change in abundance of *glutinosus.*	Means that original hypothesis of competition was false. Total distribution pattern hard to interpret. Expect other bad results. Habitat disturbed?
		b. Increase in abundance of *glutinosus.*	Confirms original hypothesis of competition. Should increase more than in A 2 b of Table 1.
B. Remove *glutinosus.*	1. Leave local *jordani* alone.	a. No change in abundance of *jordani.*	Means that original hypothesis of competition was false, especially with A 2 a. (Same interpretation)
		b. Increase in abundance of *jordani.*	Confirms original hypothesis of competition; *jordani* should increase more than in B 1 b of Table 1.

SPECIALIZATION AND THE RESULTS OF ECOLOGICAL INTERACTIONS

The evolutionary result of competitive interactions has been the subject of a great deal of speculation, most of it stressing specialization for different resources. This interpretation requires scrutiny, since it implies that differential specialization is a probable result of competition for resources, and the observation of different food habits among coexisting related species has been interpreted as avoidance of competition.

Such an interpretation, to be accepted even provisionally, should require an examination of alternate hypotheses to explain the observation. One such hypothesis that has not been explored adequately, is that specialization carries advantages in efficiency of handling, digesting or metabolizing the food, and that competition need not be invoked at all. Thus, competition is easily shown not to be a necessary condition for the evolution of food specialization. The subject will be pursued to examine the question of the sufficiency of competition as an explanation. If specialization for one kind of food is regarded as a derived state, as either of the above hypotheses assumes, then polyphagy must be regarded as the starting point for any reconstruction. Assuming that such is the case, and that the members of a species are experiencing intraspecific competition for food, an individual of this species which tended to specialize would be at a disadvantage whenever its specialty became scarce, since, in becoming a specialist, it would be expected to lose some ability to handle or digest the remaining kinds of food. The only ways for such a specialist to remain at an advantage would be to begin by being so efficient at obtaining the special food as to overcome the expected periodic scarcity, or else in some way to avoid the expected trade-off in efficiency with regard to other kinds of food. The probability appears to be very low in either case. Thus, for food-limited species polyphagy should be the rule.

With an initially polyphagous species that has a superabundant supply of food, the situation is quite different. Any genotype increasing specialization is likely to be favored because of the benefits of increased efficiency. No penalty is attached to this tendency, because under the terms stated, none of the various kinds of food is ever in short supply. Therefore, contrary to routinely accepted theory, specialization for different foods should be characteristic of species that are not in competition, and the claim is hereby advanced that prior competition is neither a necessary condition nor a sufficient one to explain the coexistence of closely related species each specializing on a different food.

How is such a claim to be tested? One way would be the laborious one of field experimentation testing for the means of limitation of population size in a large series of related species, some of which were monophagous and some polyphagous. If the former are consistently limited through means other than the supply of their food resources, and the latter show a consistent tendency to be food-limited, the claim would be strongly supported. Rigorous proof of a series of events in evolutionary history is, of course, not possible, and in the present instance, even if the experiments had the expected outcomes, the counterclaim could always be made that the specialists had been released from competition by becoming specialists and therefore would have to be limited in abundance by some other factor.

A *post facto* test of the claim that food specialization implies the absence of prior competition for food can be suggested in the following manner. Among a number of species whose food is well documented, there should be no particular relationship between the degree of specialization and the number of specialized species per species of food. If, on the other hand, specialization represents an evolutionary "escape" from competition for food, the advantage gained should be reflected in a tendency to be the only such species feeding on the food species in question. Thanks to an extensive table by Needham, Frost and Tothill (1928), this test can be made in the case of leaf-mining insect species. There are 435 species of plants that serve as hosts. Of these 289 are fed on by only one species of leaf miner; 82 are fed on by two species, and 64 are fed on by three or more species of leaf miners. On the hypothesis that the distribution of the insect species is by chance among the three groups of plant species, the expected distribution can be calculated by tabulating for each insect species its host plant species with respect to the number of insect species that the host plant supports. Thus, for each specialist, only one plant species will appear in the table; for those feeding on two plant species, both plant species will appear in the table, and the same system continues for insects feeding on three or more species of plants; each plant species will appear separately in the appropriate part of the table. After the removal of those records involving plants determined only to genus, and prorating those appearing more than once in the table, there remain 426 records of the plant species, classified according to

TABLE 3. The number of species of plants attacked by varying numbers of species of leaf-mining insects. The insect species have been separated according to the specificity of their food habits. The figures in the table have been calculated on the assumption of no relationship between the degree of specialization of the insect and the number of species of insects supported by its food plant (s).

Number of species of host plant per species of insect	Number of species of insect per species of host plant		
	1	2	3 or more
1	99.47	28.31	21.87
2	47.21	13.44	10.38
3 or more	136.41	38.83	30.00

TABLE 4. The observed distributions of plant species for comparison with the expected distributions in Table 3.

Number of species of host plant per species of insect	Number of species of insect per species of host plant		
	1	2	3 or more
1	94.00	37.50	18.31
2	48.00	11.00	12.10
3 or more	134.00	38.50	32.95

the number of insect species feeding on them. In the absence of a relationship between specificity of feeding by the insect and the number of insect species supported by the host, these 426 records should be distributed in the ratio 289 : 82 : 64 for each group of insects: those found on one species of plant, those found on two species and those found on three or more species. The expected distributions are given in Table 3.

If specialized species of insects tend to specialize on plant species for which there is little competition, there should be an excess of species in the first column for species with one host, and a corresponding deficiency in the third column for the same row. That such is not the case is shown in the observed distribution (Table 4). Three of the specialists are confined to a plant species that supports them and ten other species of leaf miners; four are confined to a plant species that supports them and eight other species of leaf miners. At the other end of the scale, one species of leaf miner which lives on 37 different plant species is the only species feeding on 19 of these plants. Thus, these data provide no support for the hypothesis that specialization for specific food items arises as a direct result of interspecific competition, and the data do support the hypothesis that such specialization arises in the presence of ample food of various kinds. The data, incidentally, are also consistent with other kinds of evidence indicating that the terrestrial herbivore trophic level is predator-limited as a whole (Hairston, Smith, and Slobodkin, 1960).

It is now worthwhile to examine the kinds of divergence that would be likely under the selective force of interspecific competition. It is assumed, and will probably be conceded, that competition is likely to be most intense between close relatives, here interpreted as those most recently separated by speciation. It is further assumed that newly separated competing species will be in contiguous but largely nonoverlapping ranges. If the differences between the adjacent places were great enough, the process of adaptation to the separate local conditions would be likely to result in species that were different in many ways, including the acquisition of different kinds of food, even if both species were limited in abundance by their food supplies. Selection might now favor either of two quite different courses: the production of competitive mechanisms specifically against the neighboring species, or further divergence by each species in obtaining food in those parts of the others' range most like its own. The first would sharpen the boundary between the two species, as is the case with *Plethodon jordani* and *P. glutinosus* over parts of their distribution; the second course would be expected to lead to broadly overlapping but different ecological distributions, such as are exemplified by the species of *Desmognathus*. These two courses, as well as the third and noncompetitive course proposed earlier, would have quite different consequences from the standpoint of systematics. The continued highly competitive situation should result in few differences, and it is easy to imagine situations in which hybrids would be at an advantage. The two species of *Plethodon* in the Nanthala Mountains may provide an example. Where the species become differentially adapted to place, it would be expected that many differences would be favored, and that eventually these would become the large differences that characterize higher categories. It would be easy to place *Desmognathus aeneus* and *D. quadramaculatus* in different genera, were it not for the existence of two species intermediate between them in morphology. Finally, in the noncompetitive situation, it might be expected that selection would produce few differences, but those would be very distinct, and would be such as to put hybrids at a severe disadvantage.

What is being suggested here is that an analysis of the systematic and distributional relationships provides clues to the ecological forces that have been operating on the species in question. In the case of one such situation, there has been proposed a series of experimental tests designed to permit a choice among the ecological and selectional events that led to the present systematic relationships. Without such planned experiments, we are committed at best to accepting "natural experiments," the conditions of which may be unknown to us, and which nearly always lack the elements of controls and of experimental design that promote definitive answers to specific questions. Manipulations will not be possible for all situations, but if the different ecological causes and their systematic effects that I have suggested can be confirmed for a few specific cases, predictive power would be added to the simple analyses to which we are now confined.

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THE EVOLUTION OF BEHAVIOR AND THE ROLE OF BEHAVIOR IN EVOLUTION

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Abstract. Modern behavior studies are, or should be, primarily concerned with problems of causation. The immediate causes of particular behavior patterns are being analyzed at the physiological and biochemical levels. The ultimate causes, selection pressures, are being studied by ecologists and ethologists. Unfortunately, there is little contact between the two lines of investigation at the moment. Doubtless a new synthesis will be achieved in the future. It does not, however, appear to be imminent. In the meantime, the results of behavior studies in the field or in the laboratory in semi-natural conditions can still be of use to the evolutionary biologist. They may be most helpful in revealing the details, mechanics, of certain ecological processes, which are themselves the regulators or determinants of evolutionary events. Some examples from recent work on cephalopods, monkeys, and birds may illustrate the sorts of data that are both available and relevant.

Introduction

I have been asked to talk about my own work on animal behavior and related subjects, and also to say something about possible further developments of behavioral studies in general. The prospect of thus anticipating the future is not entirely gratifying. It seems to me that current research on animal behavior has reached a difficult, awkward, almost embarrassing stage. As is the case with any subject, there are numerous false starts and unrewarding pursuits. Some questions being asked by workers in the field are hardly worth posing. The answers are self-evident or easily predictable. Some other questions are devoted to more significant problems, but apparently cannot be answered with the techniques currently available, at least not the techniques actually being used. More important, the various kinds of studies that are proving to be useful and successful are becoming increasingly disparate in both methods and objectives.

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This anomalous situation is, of course, the result of historical factors. It might be instructive, therefore, to give a brief résumé of some aspects of the past, in order to explain the present unease and to provide or reveal a reasonable rationale for some of the continuing work — my own included.

Many biologists, the majority of evolutionary biologists and "natural historians," probably would agree that the most stimulating school of behaviorists in this century was that of the "ethologists." Ethology as such may be difficult to define. In theory, the term could be applied (without paying too much attention to its classical derivation) to the whole of the science of behavior. In fact, it is usually restricted to a particular approach to the subject, based upon Darwin (1872) and other pioneers such as Heinroth (1911), Whitman (1899 and 1919), Huxley (1914), and Craig (1918), and perhaps influenced by some early ideas of Freud or his predecessors, but largely developed in continental or Teutonic Europe in the 1930's and 1940's and subsequently widely diffused, first in the English-speaking world and then elsewhere in the next decade.

This school was distinguished by a concentration upon large segments or sequences of behavior in natural or semi-natural conditions, especially social (inter-individual behavior and the reactions that were called at the time "innate," *i.e.,* species-typical or (often by implication) species-specific. Among the better known products of the school which may serve to illustrate its original range of interests were papers by Lorenz (*e.g.,* 1931, 1935, 1941), Lorenz and N. Tinbergen (1938), N. Tinbergen (1932, 1935, 1936, 1939, 1940), Makkink (1936), Kortlandt (1940), Seitz (1940 and 1941), and Baerends and Baerends (1950).

Another characteristic of the first ethological studies was a preoccupation with causes, not only long-term components such as selection pressures affecting behavior in the course of evolution but also short-term or even immediate causes, external and internal states and stimuli and internal mechanisms producing particular acts at particular instants in time. The latter interest entailed a considerable amount of rather ambitious and detailed model-building, the development of concepts and terms such as "Innate Releasing Mechanism," "reaction specific energy," "displacement" activities, and "hierarchies" of instincts. The state of the art at this stage is beautifully summarized in N. Tinbergen

(1951). Unfortunately, most of the models proved to be descriptive of the overt manifestations of behavior but not explanatory or usefully predictive. They did not correspond very closely to the actual events within a behaving animal. (This sort of discrepancy between the perceived and the real is an occupational hazard of model-building. There may be comparable gaps in ecological models — a topic that will be mentioned later.)

The responses of ethologists to their logical and methodological difficulties were exceedingly diverse:

1. The original mainstream of effort was impeded and reduced but did not dry up completely. There were hopeful and ingenuous attempts to redefine and refine the classic concepts (see, for instance, Bastock *et al.,* 1953; Hinde, 1954a and 1954b; Morris, 1957; Blest, 1961). Some of these attempts may have been helpful in minor ways, but I think that it would be fair to say that they did not do very much to resolve the basic dilemma. There was a push to render descriptions more precise, by adoption of mathematical and pseudo-mathematical means of notation, often with an infusion of information theory and cybernetic terminology, and by increased use of improved photographic and other kinds of recording equipment. Examples are too numerous to cite, but many can be found in recent issues of the journals "Behaviour" and "Animal Behaviour" and the bibliographies of the general surveys of Hinde (1970), Eibl-Eibesfeldt (1970), and Marler and Hamilton (1967). All too often, they have merely told us what we already knew or assumed, at distressingly greater length and elaboration than we were prepared to cope with.

2. Perhaps a more practical response was switching of attention to groups of animals and special problems that had been neglected in earlier years. Several bends in the river or new channels which are in some danger of becoming oxbows but are at least picturesque. There has been a great deal of strictly ethological work on a variety of "lower" mammals such as marsupials, rodents, and carnivores (*e.g.,* Kaufmann, in press; Kleiman, 1972; Leyhausen, 1956; Kruuk, 1972; Schaller, 1972; Ewer, 1963, 1968, and 1973), and an enormous proliferation of studies and surveys of primates (*e.g.,* Altmann, 1967; Chance and Jolly, 1970; Crook, 1970; DeVore, 1965; Dolhinow, 1972; Imanishi and Altmann, 1965; Jay, 1968; Jolly, 1966 and 1972; Kummer, 1968 and 1971; van Lawick-Goodall, 1971; Morris, 1967a; Moynihan, in press a; Petter, 1962; Poirier, 1972; Reynolds, 1968; Rosenblum and Cooper, 1968; Rowell, 1972;

Schaller, 1963; Struhsaker, 1969). Many of these papers were indirect reflections of a strong interest in human behavior, both as it is and as it may be supposed to have been at some earlier time in the Pliocene or Pleistocene; and there have also been attempts to apply conventional ethological insights to some of the urgent problems of modern man (*e.g.,* Lorenz, 1963; Russell and Russell, 1968; Morris, 1967b; Martin, 1972) with amusing results (critics have tended to dismiss both the good and bad suggestions and interpretations as impertinent *sensu stricto,* but it may be hoped that some of them will eventually be incorporated into the intellectual background of the well-informed citizen).

The most fashionable of the special subjects has been what might be broadly called "communication." Different aspects of the subject have been tackled at many different levels and in many different areas. There have been analyses of the various ways in which information, true or false, can be transmitted among individuals of the same or different species, and also of the means by which transmission can be prevented or interrupted. One of the aspects of interspecific communication that has attracted investigation and speculation is mimicry, not only the long known Batesian and Mullerian types but also aggressive and social and even more recondite forms. Relevant publications include Brower *et al.* (1960, and many other papers from the same school); Rand (1967); Robinson (1969); Moynihan (in press b), and an extensive discussion and summary in Wickler (1968). The methods by which predators discover and recognize prey, with or without the baffles of mimicry and crypsis, have been studied by many workers. The papers of Robinson and his collaborators (*e.g.,* 1969, 1971a, 1971b) reveal some of the factors that may come into play. Research on intra-specific communication has been primarily concerned with the even more variegated "languages" used in more complex social situations ("social" in the every day sense of the term). It has involved description, decipherment, and efforts to detect and formulate the general rules, the "grammar and syntax," of a multiplicity of signal systems. There have been surveys and comparisons of the signals of different groups of animals (*e.g.,* Tembrock, 1959; Lanyon and Tavolga, 1960; Busnel, 1963; Sebeok, 1968), somewhat abstract discussion of theory (*e.g.,* W. J. Smith, 1965 and 1969; Moynihan, 1970; Cullen, 1972; Mackay, 1972), and detailed accounts of particular systems, ranging from the pheromones of insects (*e.g.,* the work of E. O. Wilson and his colleagues) through bird "song" (*e.g.*, Thorpe, 1961; Hinde, 1969) to the non-verbal movements and expressions of children and adults in contemporary western and other human societies (*e.g.*, Goffman, 1971; Blurton Jones, 1967 and 1972; Argyle, 1972; Eibl-Eibesfeldt, 1972). These studies may have implications for related fields. They have, for instance, at least made available to "real" linguists such as Chomsky, Lenneberg, etc., some useful background material and evolutionary perspective.

3. However valuable such works may be, they would appear to be diversions from the classical behavioral point of view. Most active students are proceeding, and probably will continue for the foreseeable future, in one or the other of two different directions, two new mainstreams. Those who are preoccupied with immediate causes are going into physiology in earnest, laboratory research on hormones, nerve cells, receptor organs, at the deepest or lowest, even molecular, level. I cannot say anything about this. Results are obviously flowing in, but the subject is complex and not my major interest and I am not competent to discuss it.

4. Ethologists who are more concerned with ultimate causes are exploring connections or interfaces among behavior, ecology, and evolution.

This has been my own preference. I may, therefore, be able to illustrate some of the positive virtues and negative drawbacks of the approach by citing particular cases from my own experience. In recent years, I have been engaged in observation and analysis of three groups of animals, cephalopods, New World primates, and passerine birds (and some "near passerines" such as hummingbirds), in the field in natural or semi-natural conditions.

EXAMPLES

1. I was attracted to cephalopods for several reasons. They provide remarkable examples of evolutionary and ecological convergence. Beginning with a molluscan body plan, they have acquired large size, good eyes, large brains, and (in many species) active and predatory habits. They have become similar to many fishes and other aquatic vertebrates in these respects. (The convergence is discussed at length *in* Packard, 1972.) They have also evolved unique or peculiar characters such as distinctive methods of buoyancy control, color changes, and jet propulsion. Combinations of some of these features have finally

allowed them to invade the laboratory, to serve the neurophysiologist. I would say, without being an expert, that some of the operations of their central nervous systems and their handling of visual information must be better known than the corresponding processes of any other animals with the possible exception of man. See, for instance, Young (1964 and 1972), Wells (1962), and the many papers of Sutherland and his co-workers.

In these circumstances, it is noteworthy that the social behavior of cephalopods has not been studied in anything like the detail that might, off-hand, have been expected. (There are technical reasons for this comparative neglect. Most cephalopods do not live long in captivity and/or are difficult to follow in the field.) Such work as has been done on the subject has been unevenly distributed. The great majority of living species of the class can be assigned to one or the other of three diversified and flourishing orders. Using the terminology of Jeletzky (1966), these may be called Teuthida (including the squids), Sepiida (cuttlefishes and their relatives), and Octopida (octopi and argonauts). There are more or less lengthy published accounts of the social behavior in the laboratory of the common European cuttlefish, *Sepia officinalis* (L. Tinbergen, 1939; Holmes, 1940), and the common octopus, *Octopus vulgaris* (*e.g.*, Packard and Sanders, 1971; Wells and Wells, 1972), but relatively little on other species, only bits and pieces on some reactions of a few other sepiids and octopi and several kinds of squids, mostly *Loligo* spp., in the laboratory or in the field (see references *in* Lane, 1957, and Moynihan, in press b).

I was delighted, therefore, to encounter a species of squid, *Sepioteuthis sepioidea*, in the San Blas Island region of the Atlantic coast of Panama which is quite unusually easy to observe in the wild under natural conditions. Mr. Arcadio Rodaniche and I seized the opportunity to look at its social behavior. We have now been observing it at monthly intervals for over two years.

The species occurs inshore in moderately or very shallow waters over turtle grass and coral. It is often extremely abundant. It is a true squid, but rather cuttlefish-like in shape, adapted for "hovering," and much less rapidly or continuously mobile than most other squids (see also Boycott, 1965). It is both predator, eating small fishes and crustaceans, and prey, being eaten by large fishes such as barracuda and snappers (and perhaps many other animals, including birds, Brown Pelicans, etc.). Individuals of the species tend to scatter singly or in pairs or trios to hunt more or less actively at night, but they congregate in large groups in the daytime to wait for prey to come to them. The daytime groups may be almost completely stationary for long (several hour) periods. Even when they are less sluggish, they tend to keep within rather small territories or home ranges. Groups are easily habituated to the presence of human observers. (In fact, one of the few technical problems of working with the species is to keep from getting too close to retain perspective and an overall view.) Individuals in groups are not shy about performing a variety of elaborate social reactions, including the full range of "courtship" and copulatory patterns, before human observers. Thus, they have provided us with a superfluity of data.

What have been the results?

In one sense, they have been disappointingly conventional. The social behavior of *Sepioteuthis* is essentially vertebrate-like in basic articulation and organization. There do not seem to be any general principles of molluscan behavior apart from those shared by most other complex animals of other phyla. But this squid does exhibit or illustrate a whole series of interesting special adaptations which may be correlated with, causally related to, one significant aspect of its ecology — and many of which may also be characteristic of other cephalopods and for the same reasons.

S. sepioidea populations are highly structured. Not only do individuals repeatedly leave and rejoin groups, but even the groups are formed of sub-groups which may be separate at some times, with obvious hostility and territorial defense among themselves, yet completely integrated at other times. There also are size and (presumably) age classes that assort themselves in particular spatial arrangements according to particular temporal and physical circumstances. The system is both intricate and flexible, apparently at least as much so as those of such mammalian carnivores as lions, African hunting dogs, and Spotted Hyenas.

The system is mediated by signals, both ritualized (mostly displays) and unritualized. As far as we can tell, all the signals are visual. (Cephalopods seem to be deaf, and we did not detect, see, any indications of the use of pheromones or other means of olfactory communication.) The visual signals include postures and movements and many color changes. The number of ritualized patterns is quite high. The basic components of the ritualized repertory may not be more numerous than the corresponding elements in the repertories of certain birds and fishes (see Moynihan, 1970), but they can be combined and recombined almost endlessly. It is not uncommon to see an animal adopt two or three, even four or five, color patterns simultaneously, each color on a particular part of the body, while performing a series of movements, especially of the fins or arms, in very rapid succession. The effect is Protean. A squid is quite able to transmit a variety of different signals in different directions to different receivers, different kinds of onlookers, all at nearly or completely the same times. As visual signal systems go, the cephalopod versions must be unique in their combinations of speed and diversity or multiplicity and perhaps efficiency.

Comparison of the known patterns of *Sepioteuthis, Sepia, Octopus,* and some other cephalopods has revealed some suggestive similarities and contrasts. Some displays are very distinct, obviously not homologous, in the different species. Others are very similar. Some of these are relatively simple. They may well have become ritualized independently in each of the phyletic lines. But at least four major displays are both extremely complex, exaggerated, and "unexpected," and yet strikingly similar in many details (of causation and function as well as form) in the various species. These displays would appear to have become ritualized before the lines diverged from one another. As the divergence must have occurred well before the end of the Mesozoic, perhaps most probably in the Late Triassic, the patterns are not only old but also have been remarkably conservative during evolution. To my knowledge, they have been more conservative than any patterns of other groups so far recorded in the literature. One of the reasons why some or all of them have been stable is apparent when they are compared with the other displays of the same species that have changed more considerably or developed more recently. The latter tend to be shown to only a few individuals or types of individuals. The conservative signals, on the other hand, are designed to influence a great number and diversity of receivers, different age, size, and sex classes of the same species and/or individuals of other species, especially potential predators. This may be a general rule, applicable to most animals. All other things being equal, the more widely reflected or broadcast a signal, the more conservative it will be, the more narrowly reflected or broadcast, the more likely it is to be changeable in evolutionary time.

The role of predation should be emphasized in connection with cephalopods. There is good evidence (see Moynihan, in press c) that several or many of the living members of the class are favorite prey of marine birds and mammals almost throughout the seas and oceans of the world. They must, therefore, be themselves enormously abundant in many areas. (Common as it is, *Sepioteuthis* has a fairly restricted distribution in the tropical Atlantic. Other squids must have larger populations. The total numbers of cephalopods in any given area are difficult to estimate precisely, as many species are nocturnal and most are difficult to catch with the traditional gear of marine biologists, but the birds and mammals probably are more efficient collectors.) There also is evidence that the enormous biomass of cephalopods is divided among fewer "packets," *i.e.,* species, than is that of their nearest competitors, the marine fishes. This could be both cause and consequence of their relatively greater attraction for predators.

It may be assumed that many of the extinct cephalopods exhibited some or all of the demographic and ecological characteristics of their living relatives. If so, it seems likely that predation pressure could have been the major impulse for a series of evolutionary events. Some of the probable steps can be listed briefly and crudely. The ancestors of the majority of living cephalopods presumably reduced, internalized, and in some cases lost, their originally external shells to gain greater maneuverability and powers of escape. This "freed" their skin for other uses, including the elaboration of color change mechanisms. The development of gregarious habits may well have been another (even earlier?) anti-predator adaptation (Brock and Riffenburgh, 1960). The habit of living in groups puts a premium upon the development of complex signal systems. For vulnerable marine animals, a visual communication system has definite advantages. (Visual signals can be turned off instantaneously whenever necessary or desirable, unlike olfactory cues, and they are perhaps less apt to be noticed at a distance by dangerous receivers than are acoustic signals, especially in murky waters or around reefs or vegetation. And, of course, short range signals are perfectly adequate as long as the animals are close together.) Once the skin has become specialized for color changes, it probably is not easily transformed for other purposes such as the development of new kinds of armor or spines. This restricts the choice of further anti-predator adaptations. It has already been mentioned that whatever displays may have to be shown to potential predators are conservative. As many or most of these patterns are also used in intraspecific encounters, they may tend to impede fundamental changes in the type, although certainly not the details, of the signal system as a whole. Other characters of cephalopods such as their rapid growth, relatively short life spans, special arrangements and care of eggs (see, for instance, Packard, *op. cit.,* and Wells, *op. cit.*), and even their preference for reproducing only once in a lifetime, in "big bangs" (Gadgil and Bossert, 1970), could also be explained as responses to intense predation. (And the need to synchronize reproductive moods in a hurry, without much time for trial and error, must add another premium for both gregariousness and the elaboration of signals.)

The series is an illustration of some of the ways in which ecology and behavior can interact to determine the course of evolution, each step opening up some possibilities and foreclosing others.

2. The New World primates are a variegated family of monkeys of some 11 to 13 genera and many species. I have observed representatives of all the genera at irregular intervals over 15 years. Some species have been observed only in captivity, at the field station on Barro Colorado Island and in zoos in Washington, London, Paris, and Amsterdam; but many others have been studied at considerable length in the wild, in the central part of the isthmus of Panamá, to the west in the province of Chiriquí, and to the south in the upper part of the Amazon basin, in the Caquetá and Putumayo regions of Colombia.

For most biologists, the primary significance of the American monkeys is that they represent a wide and independent adaptive radiation. They have occupied most of the habitats available to primates. In this respect, they are more or less strictly equivalent to the two other radiations of modern primates, the (Recent and Pleistocene) lemuroids of Madagascar, and the so-called Old World monkeys and apes, the "Catarrhini," of tropical Asia and Africa and some adjacent areas, of which man is a specialized offshoot. The New World forms may thus provide a useful check to hypothesis and speculation about the evolution of primates in general and man in particular. I should also like to claim that they are interesting in themselves.

They range from very small (the Pigmy Marmosets of the genus or sub-genus *Cebuella*) to moderately large (the howlers, *Alouatta,* and the spider monkeys, *Ateles*). They show a great diversity of types of locomotion, from squirrel-like scrambling and/or vertical clinging and leaping among the marmosets and tamarins (*Saguinus, Leontideus, Callimico,* and *Callithrix* in addition to *Cebuella*), through quadrupedal "springing," walk-ing and pacing in such forms as *Saimiri* and *Cebus,* to brachiation or semi-brachiation with the supplementary use of a prehensile tail in *Ateles.* (The classification and details of locomotion are discussed *in* Erikson, 1963, and Napier and Walker, 1967.) At least two species of *Cebus, capucinus* and *apella,* come down to the ground with appreciable frequency. All or most of the species of other genera are thoroughly arboreal. One genus, *Aotus,* is nocturnal; the rest are diurnal. They all tend to be nearly omnivorous on occasion; but most of the smaller forms, many of the tamarins and probably the marmosets of the genus *Callithrix,* seem to prefer insects whenever they can get them, while some of the larger forms are essentially herbivorous, taking various assortments of fruits of particular kinds and ages, as well as buds and leaves and even twigs and bark. At least one form, *Cebuella,* has specialized in sap-sucking. (The sap-sucking is described *in* Moynihan, in press d. The best general accounts of more conventional feeding habits and régimes, unfortunately limited to the Panamanian species, are *in* Hladik and Hladik, 1969, and Hladik *et al.*, 1971.)

In the course of my own studies, I have attempted to discover and analyze the social behavior and structures of different species and combinations of species, to determine how such complexes are held together (or apart as the case may be), and to identify some of the selective forces involved, to tie the observed behavior to particular aspects of ecology. The results summarized below are taken from Moynihan (in press a); this book also lists references to papers and unpublished notes of other workers.

Two extreme types of intraspecific social organization can be recognized without much difficulty: the restricted "nuclear" family group and the large band. The former seems to be the basic social unit of *Aotus, Callimico;* two species of *Callicebus, moloch* and *torquatus;* and, in some circumstances, *Pithecia monacha.* Bands are characteristic of *Pithecia melanocephala, Alouatta villosa, Alouatta caraya, Lagothrix, Saimiri,* and some or all forms of *Cebus* and *Ateles.* As might be expected, there are intermediate conditions, complications, and exceptions. One type of intermediate is the "extended" family of some species of *Saguinus, e.g., fuscicollis, graellsi, midas,* and *Cebuella* and probably many other marmosets. Intermediates can also be flexible, intermittent or recurring. Small families of some species may join one another in some circumstances. It also is normal or usual for neighboring small families of most species to perform certain responses, *e.g.,* anti-predator reactions, in common. (This is evidence that they do form a real social community.) Conversely, large bands may split up into smaller sub-groups temporarily, or reveal traces of sub-group organization within the bands without actual splitting. This appears to be most common in *Saimiri* and some form of *Ateles.* (The sub-groups are not usually families but rather cephalopod-like age and sex classes.)

The adaptive value of such variance is surprisingly obscure. It seems to be characteristic of American monkeys that there is little general correspondence between basic types of intraspecific organization and either habitat or food preferences. There are species that live in bands and species that live in small family groups among the primarily or exclusively vegetarian forms. There also are both kinds of species, or at least forms that usually live in bands and forms that live in extended family groups, among the animals that prefer insect food when available. The proportions of highly to poorly gregarious species and individuals are much the same in many of the stages of succession from young second-growth scrub to mature forest in many areas. Perhaps even more remarkable, density of populations also appears to be largely irrelevant in this connection (if not for other aspects of social behavior — see below). Both *Callicebus moloch* and *Saimira* usually are abundant and concentrated wherever they occur. They are concentrated in different ways, but the average number of individuals per unit of time and area may be high in both cases. Both *Aotus* and *Cebus albifrons* can be described as dispersed. The *albifrons* occur in rather large bands, but the bands themselves are scattered.

These facts would suggest that almost any type of social organization can permit or facilitate almost any kind of exploitation of the environment within the range of niches occupied by American monkeys at the present time. Presumably, because most of them are more "generalists" than "specialists," they have been able to choose among alternative strategies to achieve similar ends.

Much more restricted are the modalities or techniques by which particular social systems are maintained. The ritualized signal systems of these animals are not only adaptive but are quite obviously so, down to the finest details. They include visual, acoustic, olfactory, and tactile patterns (Moynihan, 1967). Of these, the visual and acoustic seem to be usually most important. The basic elements, the deep structures, of the repertory of sounds may be nearly identical in all species, with the possible or probable exception of *Alouatta.* It is not difficult to trace homologies among most of the vocalizations of most of the species, and much of the information encoded is almost uniform or strictly equivalent throughout. The forms and frequencies of particular patterns are, however, very different in different species. The differences seem to depend upon the distances over which sound usually need to be transmitted, the carrying properties of the medium (the numbers and kinds of obstructions likely to be encountered), and the presence or absence of other possible sources of relevant information, features of the external and/or social circumstances and other types of signals. In fact, this means that both the physical forms of the patterns and the methods of encoding information are closely correlated with social structure, density of population, activity rhythms, and density of vegetation, as well as vulnerability to predation and diversity of appropriate receivers. The ritualized visual signals are more heterogeneous but equally easy to explain in terms of the same factors.

Some New World primates are involved in, or are the foci of, specialized and stereotyped interspecific social reactions. Such reactions may take either positive or negative forms, "friendly" joining and following or hostile fighting or avoidance. They may occur among two or more species of monkeys and/or between monkeys and other animals such as squirrels (*Sciurus granatensis, S. variegatoides, Microsciurus* sp.), birds of prey such as *Harpagus bidentatus* and *Leucopternis albicollis* (these small hawks do not attack the monkeys themselves, but rather take the arthropods, lizards, etc., flushed by them), and even flycatchers (*e.g., Myiozetetes, Tyrannulus, Lagatus, Elaenia, Megarynchus*). The combinations of positive and negative responses can be complex, and the interspecific relations of a single species may be different in different areas. It is possible, nevertheless, to detect certain general rules or trends.

There are apparent correlations among interspecific bonds, feeding habits, and territorial behavior. The monkeys that are most likely to mingle with other species are forms such as *Callicebus moloch* and *Alouatta villosa.* They are vegetarian, taking items such as leaves, buds, and berries that are abundant and evenly distributed, and have small territories or large territories through which they move slowly. Individuals and groups of these species seldom find themselves in situations with which they are not thoroughly familiar or have not had time to inspect carefully beforehand. Conversely, the establishment of friendly interspecific bonds is characteristic of such forms as *Saimiri, Cebus apella,* and *Ateles paniscus s.l.* They are omnivorous or preferentially insectivorous or feed on plant materials that are dispersed or distributed in irregular clumps. They tend to have large territories through which they move rapidly. They must be precipitated into unfamiliar situations rather frequently. They must also, therefore, have more need of extra companions of the same or other species, to act as scouts or sentinels, than do species of more sedentary or cautious habits.

On logical grounds, one would suppose that the various kinds of interspecific social behavior should be adjusted to intensities of competition[1] as well as particular ecological facies. It would be expected that species that do not compete at all, or compete as little as may be feasible for animals that occur in the same areas, would usually tend to ignore one another. There are many apparent examples of such behavior among the New World primates. It would also be expected that species that compete very strongly would tend to exclude one another from wide areas and entire regions. Again there are apparent examples among the American monkeys.

Presumably either of these extreme types of interspecific behavior can be transformed into the other in the course of time. It would be interesting to know the intermediate stages. Data from observations of the New World primates and their associates would suggest that the following progression (quoted from Moynihan, in press a) may be common as intensity of competition increases: "When competition becomes slightly more than minimal, the species will tend to ignore one another in most circumstances but will exhibit overt and active hostility toward one another occasionally. (If it is only desirable or necessary to drive off rivals infrequently, it may be worth taking the risk of fighting.) When competition is stronger, it may be advantageous for the competitors to join up with one another. (If you can't lick 'em . . .) When competition becomes stronger yet, it may become imperative to avoid one another. First by avoiding personal encounters while still ranging over the same areas at much the same times. Then by claiming exclusive territories or by elaborating some form of temporal segregation. (Segregation by differential timing may have peculiar advantages, but it can only work when the species involved are not too numerous.) From the claiming of exclusive territories, there may be no more than a small step to complete allopatry. It seems very probable that the process can also go in the opposite direction, through the same stages but in reverse order, and that the direction of change can be reversed repeatedly, with or without reaching the extreme conditions at either end."

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[1] I am employing such terms as "complete" and "competition" in the broadest possible sense. Two animals are considered to be competing with one another whenever one preoccupies, permanently or temporarily, any resource that would otherwise be likely to be used by the other. Among primates and birds, competition for preferred observation posts, singing perches, safe sleeping quarters, etc., may be quite as important as competition for food.

3. Most of my recent work on birds has been conducted in the Andes.

The higher reaches of these mountains provide a wealth of material for students of biogeography. They include a large series of habitats and biotas that differ from those of the surrounding lowlands in several respects (*e.g.*, temperature, endemic species). The northern part of the Andes is extremely complex in structure, with separate cordilleras, chains of mountains, and a scattering of single peaks and massifs. The central and southern parts are simpler, more unified in general or overall form, but still varied in details of terrain and climate. As a result, many of the higher altitude habitats and biotas are distributed in patches, partly or wholly isolated from one another. They are essentially insular. They differ from oceanic islands, however, in not being impoverished. The higher Andes have "complete" or "balanced" floras and faunas. They are inhabited by many kinds of organisms which have occupied most of the obvious niches or ecological roles, exploited most of the available opportunities. They are, therefore, ideal for analyses of some aspects of insular evolution. The effects of isolation and adaptations to facilitate or impede invasions can be studied *per se,* quite apart from the possible distortions of "accidental" barriers or "sweepstake" phenomena.

I have concentrated upon interspecific behavior among two groups of species of a particular "life zone." Observations were begun in 1959 and have continued off and on until the present. The results are being analyzed and written up. Many details remain to be settled, but the general sense of the bulk of the data is clear.

The life zone is the one that Chapman (1917 and 1926) called "humid temperate." The term is perhaps misleading — "cold humid tropical" might be more suitable (see comments *in* Moynihan, 1971). The zone is best developed around 2800–

3300 m in most areas. Its natural vegetation would be more or less dense forest and "alpine" scrub (Weber, 1969). Some of this survives apparently intact. The rest has been replaced by secondary bush, gardens, hedges, crop fields, pastures, etc. Fortunately, substantial numbers of the native birds have been able to occupy and even flourish in some (the lusher) of these man-made habitats. They are still easily observable. The distribution of the zone is eccentric within the Andes. It must cover almost the whole of the northern Andes at appropriate elevations, *i.e.*, it is scattered among islands, most of which are small, a few of which are large but long and narrow. It is much broader and more nearly continuous in the central Andes, in all or most of central Ecuador and northern Peru. It becomes progressively narrower toward the south, even though the Andes themselves remain broad. The apparent discrepancy is due both to the relief of the mountains and the nature of the prevailing wind systems (briefly summarized *in* Murphy, 1936). Rain falls off at an unequal rate. The principal southern extension of the zone is along the eastern slope of the chain, down into central Bolivia. It is dissected by the deep valleys of rivers flowing to the Amazon. In effect, the southern extremities are a series of narrowly linked narrow peninsulas.

My own observations have ranged from the Sierra de Mérida in Venezuela and the Sierra Nevada de Santa Marta in northern Colombia down through central and southern Colombia, Ecuador, and Peru to northern Bolivia, the Yungas of La Paz, at altitudes between 2400 and 3700 m. This is nearly the full length of the cold humid tropical zone, with the addition of some fringe areas of adjacent zones.

One of the groups of species studied could be called the "*Diglossa* cluster." It includes six species or superspecies of the genus, flower-piercers, which may be called *carbonaria, lafresnayei, albilatera, baritula, cyanea,* and *coerulescens* (this is the nomenclautre and classification of Zimmer, 1929; Hellmayr, 1935; and de Schauensee, 1970 — Vuilleumier, 1969, suggests a slightly different arrangement, and other refinements are conceivable), as well as the conebill *Conirostrum cinereum* and some hummingbirds such as *Colibri coruscans, Aglaeactes cupripennis,* and *Ramphomicron microrhynchum.* All these birds are nectarivorous to a greater or lesser extent.

The other group includes many more species of different subfamilies, families, and at least one more order. For want of a better name, I shall call it the "tanager cluster." It includes a variety of closely related montane tanagers, mostly black and blue with touches of yellow, buff, or red, of such genera as *Anisognathus, Buthraupis,* and *Iridosornis* (and also the "Plush-capped Finch," *Catamblyrhynchus,* hardly distinguishable from *Iridosornis* in appearance or habitus in the field[1]) ; other tanagers of rather different stocks (*e.g., Chlorospingus, Cnemoscopus, Hemispingus, Chlorornis*) ; finches of the genus *Atlapetes;* some other conebills (especially *Conirostrum sitticolor* — see Moynihan, 1968) ; warblers of the very different genera *Myioborus* and *Basileuterus*[2]; a few flycatchers (*e.g., Uromyias* and *Megacerculus* spp.) ; the occasional hummingbird (*e.g., Ensifera* and *Coeligena*) ; a few woodpeckers (*e.g., Piculus rivolii* in Venezuela) ; and many furnariids and dendrocolaptids (*Margarornis, Synallaxis, Cranioleuca,* etc.). And at least one squirrel in the western cordillera of Colombia (*Sciurus granatensis* again!). The association includes frugivores (different species taking different fruits), insectivores (catching different insects in different ways), a new nectarivores, and many types with very mixed diets. Different species also prefer different levels of vegetation, from the highest tree-tops down to the ground.

The chief peculiarity of both clusters, the one that drew my attention, is that their members show pronounced *intraspecific* geographic variation in their *interspecific* behavior. More precisely, individuals of a single species or superspecies react very differently to individuals of other species in different regions (often the same other species in each of the regions). The variation affects different types of interspecific behavior in the two clusters, hostility in the *Diglossa* association and "friendliness" in the tanager association, but the trends are roughly parallel in both, although inverse and complicated by certain exceptions. The exceptions themselves are sometimes revealing.

The situation is roughly as follows:

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[1] The classification of the "New World nine-primaried songbirds" is in need of further revision. Some of the supposed families and subfamilies of the group appear to be polyphyletic in origin. Some of the genera currently assigned to one family may be more closely related, phylogenetically, to some of the genera assigned to other families than to other genera assigned to the same family. Terms such as "warbler," "tanager," and "finch" are little more than short-hand descriptive labels for certain ecological categories.

[2] In the case of these Andean birds, it seems probable that a revised scheme would place the Plush-capped Finch in the same tribe as the tanagers it so much resembles, and also link *Basileuterus* to *Hemispingus* rather than to *Myioborus.*

Many members of the tanager cluster extend throughout all or most of the cold humid tropical zone. All show tendencies to form or join mixed species flocks in some areas and regions (this is the prescriptive reason why they have been assigned to the cluster). In general, individuals of the same species behave in similar ways in the northern and southern extremities of the zone, but very differently in the central part. They show a high degree of interspecific gregariousness in the western and central cordilleras of Colombia (the western cordillera is always extremely northern, "far out," in the behavior of its inhabitants — see also below). In these regions, the birds occur in mixed flocks most of the time, and most of the flocks are large, cohesive, complex in structure, and stable (maintained for hours on end and often re-formed on successive days). In the eastern cordillera of Colombia and the Sierra de Mérida, the birds still show a considerable amount of interspecific gregariousness, but mixed flocks are formed somewhat less frequently and tend to be smaller, looser, and simpler in structure on the average (the decline may be more evident in the eastern cordillera than in Venezuela). In central Ecuador and central and northern Peru, interspecific gregariousness is slight. In fact, quite absent in some localities. Even when and where mixed flocks *are* formed, they are always small and simple, and usually loose and sustained for only a few minutes. The trend is reversed in southern Peru and northern Bolivia. Mixed flocks become larger, more stable, cohesive, and complex again (rather more so in Bolivia than in Peru, but never as much so as in the western cordillera of Colombia).

It is obvious that the development of flocking depends upon several factors. There are positive correlations among densities of populations, thickness of vegetation, and frequency and elaboration of interspecific gregariousness within regions. But these cannot account for the whole of the major geographic trends. They do not explain the exceptions. There must be something else involved. This would appear to be an "invasion" or "frontier" effect. Interspecific gregariousness seems to go up with exposure to, or anticipated number of, invasions from or into other regions of the same life zone or an adjacent zone, the warm or hot humid zone of lower elevations.

The western cordillera of Colombia is the least continuous of the major chains of the Andes. Its patches of cold humid habitats are comparatively small. The populations of these small islands must include a relatively very high proportion of individuals near the frontiers of their patches and a low proportion of individuals at the centers of patches, away from the frontiers. The same must be true of the populations of the narrow peninsulas of the zone in the far south. Birds on the frontiers must encounter strays from other zones and stray into other zones more often than do birds from the centers. It would seem that this is one of the causes of interspecific gregariousness. The evidence is somewhat restricted, but I think convincing. In central Ecuador, I worked along one transect from the top edge of cold humid forest and scrub down into the upper reaches of warm humid forest. Interspecific gregariousness is essentially nil in the higher part of the cold humid zone, but increases abruptly at the exact point where occasional strays from the warmer zone begin to appear with some appreciable, if still low, frequency. (The increase is "intrinsic." It is always apparent, whether or not strays are present at the moment.) The remarkably high degree of gregariousness of the birds of the central cordillera of Colombia, higher than would be expected of its not particularly northern or isolated position, may also be correlated with the fact that it is exposed to invasions from the nearby chains on either side as well as from the immediately adjacent lowlands.

What is the functional significance of this apparent connection of interspecific gregariousness with frontiers, strays, and invasions? The advantages of mixed flocking from the point of view of a straying bird in an unfamiliar area are obvious, and much the same as in the monkeys cited above. By associating with experienced local individuals, a stray may be able to discover and identify food and/or danger relatively rapidly. The advantages for the "hosts" of a stranger are more problematical. Of course, they are acquiring a companion who may be of use in various ways. They are also encouraging or tolerating a competitor. Perhaps one of the reasons that they do so is that they may become strangers in their turns. Some of them must also stray into adjacent life zones, where they will also need the help of local inhabitants. It may be difficult for an animal to join and follow strangers without also developing some tendency to allow itself to be joined and followed by strangers. (The roles of joiner and joined are easily distinguishable in some areas such as parts of Panama — see, for instance, Moynihan, 1962a — but they are less clearly distinct in these Andean flocks. In any case, both roles often reflect similar states of mind.) It seems to be characteristic of most animals that they cannot, at least do not, support very great qualitative differences in kind of social responses. A species that is comparatively aggressive in one class of social encounters also tends to be aggressive in other encounters. Similarly, a species that is gregarious in some circumstances usually tends to be gregarious in other circumstances.

This "extrapolation" may have been favored in Andean birds because the boundaries of their life zones have been fluctuating, repeatedly shifting back and forth in recent geological history (see Simpson-Vuilleumier, 1971). Many of the birds of the cold humid zone must have had to invade new areas, and cope with invaders from other areas, again and again in response to secular climatic changes, quite apart from or in addition to the normal straying that would have occurred even if the frontiers had been fixed and permanent.

The species of the *Diglossa* cluster show another contrast between individuals of the central part of the cold humid zone and those of the northern and southern extremities of the zone. Some aspects of their interactions in central Ecuador have been described *in* Moynihan (1963). Each of the local species has its own, partly unique, series of ecological preferences, but the ranges of most species are broadly overlapping. The territories of individuals of different species are often completely overlapping. Individuals of different species may use the same perches, move along the same pathways, feed in the same places on the same types of foods. But they almost never do so simultaneously. They are almost always kept a few meters apart, at any given instant of time, by some avoidance mechanisms. There is also mutual inhibition of "Song" among individuals of different species of *Diglossa* and *Conirostrum cinereum,* although not among individuals of the same species. The whole thing can be summed up as rigid and continuous social segregation. In the western cordillera of Colombia and in northern Bolivia, on the other hand, many of the species are separated microgeographically, each largely or completely confined to a particular facies of habitat slightly different from the facies of all or most of the others. This may be due to fighting. On the rare occasions when individuals of different species that are usually separated do happen to come together, they usually fight, actually attack, one another. There is no visible avoidance mechanism. Thus, the micrgreographical segregation may be encouraged or imposed by reactions among individuals but it is not continuously social in the same way as in central Ecuador. Conditions are more or less intermediate in the Sierra de Mérida, the eastern *and* central cordilleras of Colombia, and many areas of Peru, with all combinations of partial overlaps, incomplete avoidance and inhibition, and more frequent and prolonged overt disputing.

The variations of the birds of the *Diglossa* cluster are also correlated with factors such as density of vegetation and interspecific competition. They do not, however, include frontier effects. They would seem to be more concerned with size of local populations and competition within regions rather than invasions by strays from without (*Diglossa* individuals are very sedentary). Individuals of the small northern and southern populations may hope to fight off all or most of their not very numerous competitors with relative ease. Individuals of the larger central population probably could not fight off their more numerous competitors without exhausting themselves in the process or taking unacceptable risks of physical injury.

It will be noticed that different adaptations for coping with interspecific competition may tend to produce different diversity gradients in the two assciations. In the *Diglossa* cluster, species diversity at any given point is least at the extremities and probably greatest at the center of the cold humid zone. In the tanager cluster, species diversity must often be greatest at particular points in the extremities and least at the center.

Comments

The sorts of work cited above are perhaps typical of a contemporary approach to ethology. I should hope that they would suggest certain conclusions about studies of behavior and the relationships of such studies to analyses of evolutionary processes.

Beginning with the purely ethological aspects, it seems evident that causation is the crucial problem. Studies of ultimate causes, natural selection, seem to be proceeding fairly well. At least, there are no theoretical or basic methodological difficulties involved. Studies of proximate causes, physiology, may also be making progress, perhaps more rapid and exciting progress. But there is very little contact between the two lines of investigation, least of all when vertebrates provide the working material. Doubtless, there will be a new and sophisticated synthesis of the two approaches at some date in the future. I do not expect to see it in my own (research) life time. I should also imagine that, when it comes, it will be largely due to an expansion of concern and efforts by physiologists. They would seem to be in a better practical position to develop the necessary techniques than are the field-oriented "natural historians."

Meanwhile, there is still a lot that the ethologist can do for for the evolutionist.

Behavioral information can help to illuminate the evolution of particular groups of animals. They have, for instance, increased our knowledge of the phylogenies of many vertebrates such as ducks and geese (Lorenz, 1941; Delacour and Mayr, 1945; Johnsgard, 1965), gulls and terns and their relatives (*e.g.*, Moynihan, 1962b), and cichlid fishes (*e.g.*, Baerends and Baerends, *op. cit.*). As taxonomic characters, however, behavior patterns are no more and no less valuable than any other characters. They may be more useful in some cases than in others, more useful than other features in some groups, less useful in other groups. They should continue to be considered, to be taken fully into account, in systematic studies. But I would suggest that they can make a more significant contribution to the analysis of evolution by providing concrete, immediate, information to help explain certain ecological phenomena, developments, and interactions which are themselves among the causes of evolutionary changes.

A substantial proportion of current and recent ecological research has been devoted to such matters as competition, coexistence, partitioning of resources, invasions of new areas and habitats, replacement, and extinction (see the works of Hutchinson, MacArthur, Wilson, and others). There has been a stimulating sequence of papers with models and diagrams, mathematical formulae and other elaborations of symbolic logic, to describe and summarize the results of interactions among individuals and species at present, as they probably were in the past, and as they may be expected to be in the future and always. What seems to me to have been lacking in many or most of these discussions is attention to some of the details of the ongoing processes as well as their end products, how and why they actually work in fact and in nature, the mechanics by which the final results are achieved. A great many questions have been left hanging in air. What do individuals of the same or different species really *do* when they come face-to-face with one another? Or when they occur in the same areas without necessarily encountering one another directly? What are the forms of competition? Who moves where, and why and when? How are specific resources found, used, preoccupied, defended? What are the relevant clues? How does replacement occur on a day-to-day or year-to-year time scale? What are the adaptations which permit or facilitate supplants and invasions? How are these adaptations used in life and why are they effective? Why are some adaptations more effective than others that could have been used instead? Is there any consistent relation between size of area inhabited and probability of success? Are there some species that are really specialists in competition? If so, why? And how do they manage it?

These are the kinds of questions which behaviorists should be able to answer, in whole or in part. I think that many behaviorists are trying to find the answers now. I hope and expect that they will continue to do so.

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MUSEUMS AND BIOLOGICAL LABORATORIES

Ernst Mayr

When Professor Crompton invited me to give a short after-dinner address on the occasion of the opening of the wing, he added that he wanted to publish it. This posed a challenge to me to come up with something that is worth being printed. However, I consider this invitation less of a challenge than a welcome opportunity to present some thoughts on museums and their role in science.

The speakers this afternoon have rightly emphasized that the opening of the Museum's laboratory wing is a milestone in the history of the MCZ. It is an occasion to look back to the days of its founding and an occasion to look forward to its future. It is also an occasion to ask some searching questions. For instance, someone unacquainted with biology and intolerant of anything but his own hobbyhorse, might ask, "Why do we still need natural history museums?" Such a question is quite legitimate, for I am a strong believer in the principle that the legitimacy and continuing value of traditional rituals and institutions should be challenged from time to time. How, then, would we answer this question?

The role of museums in science, and their image in our society, is changing from decade to decade. When natural history was revived during the Renaissance and during the 17th and 18th centuries, it expressed at first man's wonder and bewilderment at the enormous variety of life. This "diversity of nature" has been a key concept in man's world picture from the days when the Lord told Adam to give names to all the creatures in the field to the present day when species diversity is one of the central themes in the work of the ecologists.

The rich treasures brought back from exotic countries in the 18th and 19th centuries by voyages and expeditions, combined with the steady rise of a more and more scientific attitude in Western man, resulted in a changed concept of organic diversity. No longer was it merely a source of wonder but naturalists began to raise questions concerning the reasons for the existence of so many and such strange organisms and about the meaning of their peculiar distribution in Asia, Africa, the Americas, and Australia.

I am not claiming that naturalists were always interested only in the most lofty generalizations because there was hardly a naturalist who was not also infected by that strange virus called the collector's fever. Perhaps no one was more affected by this disease than the founder of the MCZ, Louis Agassiz, who cheerfully pawned everything he owned in order to acquire more specimens. Indeed, it is said that only a few decades ago this Museum still had unopened boxes of collections from Louis Agassiz's days.

These collections, however, were not merely the useless gatherings of pack rats. It was their study which helped bring about a conceptual revolution — the establishment by Darwin of the theory of evolution, to a considerable extent based on Darwin's own researches during the voyage of the "Beagle" and the subsequent working out of his collections. And the proposal of the theory of evolution was only one of several such conceptual revolutions in the history of natural history.

The diversity of nature has been considered, ever since Darwin, a documentation of the course of evolution. Research in the pathway of evolution indeed turned out to be an incredibly rich gold mine. And it was the museums that established and maintained leadership in this type of research. The historians of biology have clearly determined that the crucial advances in the modern interpretation of species, of the process of speciation, and of the problems of adaptation were made by systematists.

One of the greatest conceptual revolutions in biology, the replacement of essentialism by population thinking, was introduced into biology by museum systematists. From systematics it was brought into genetics by workers like Chetverikov, Timofeeff-Ressovsky, Dobzhansky, Sumner, and Edgar Anderson, all of whom had either been trained as systematists or had worked closely with systematists.

Again and again the students in special branches of biology such as biogeography have gone back to systematics for material and for novel ideas.

The speakers this afternoon have documented sufficiently how important museums and systematics are. But this raises another question, which is: "Why is systematics so important?" And this leads right on to the further question of the position of systematics in biology as a whole. I pointed out a dozen years ago that, in spite of all of its unitary characteristics, biology really has two major divisions; indeed, one can speak of two biologies. In the first one, functional biology, "How?" questions are the important ones. This is the biology that deals with physiological mechanisms, developmental mechanisms, metabolic pathways, and with the chemical and physical basis of all aspects of life. To use modern technical language, this part of biology ultimately deals both with the translation (decoding) of genetic programs into components of the phenotype and with their subsequent functioning. This type of biology played a decisive role in disproving conclusively all vitalistic notions and in establishing firmly that nothing happens in organisms that is in conflict with the laws of chemistry and physics. This is the biology which interprets all cellular and developmental processes, both the normal ones and such abnormal ones as the origin of cancer.

The other biology is interested in the genetic programs themselves, dealing with their origin and evolutionary change. It continuously asks "Why?" questions, for instance:

Why is there such a diversity of animal and plant life?

Why are there two sexes in most species of organisms?

Why is the old faunal element of South America seemingly related to that of Africa while the new one is related to that of North America?

Why are the faunas of some areas rich in species and those of others poor?

Why are certain organisms very similar to each other, while others are utterly different?

In the last analysis, all questions in this part of biology are evolutionary questions, and museum-based collections are ultimately needed to find the facts for posing and answering all of these questions.

At this point some of the more perceptive members of this audience will think that I have painted myself into a corner. Why, they will say, do you need a laboratory wing when the method of systematic and evolutionary biology is the comparative method, based on observations? Why do you have to perform experiments?

The explanation for the seeming contradiction is that I have told only part of the story. Systematics, as it was defined by

G. G. Simpson, "is the scientific study of the kinds and diversity of organisms *and of any and all relationships among them.*"

This definition has two consequences: First, it means that the systematist also must ask "How?" questions, like "How do species multiply?" or "How does an evolutionary line acquire new adaptations?", or "How did the phyletic line leading to Man emerge from the anthropoid condition?".

All these evolutionary questions deal with the history of changes, and, most importantly, with the causation of changes. Translated into Darwinian language, each of the questions I have just posed can also be stated in the following terms:

"What were the selection pressures responsible for causing the stated evolutionary changes?"

Not only is it often necessary to make use of experiments to answer this type of question, but, more importantly, many of such questions cannot be answered — or at least not completely — simply by the study of preserved material.

Since the investigation of diversity includes the study of relationships, organisms must be studied alive and in the field. In the last 150 years there has hardly been an outstanding systematist who was not, at the same time, an outstanding field naturalist, and who could not have been called, with equal justification, an ecologist or a student of behavior. This is, by no means, a recent development. Re-reading recently Louis Agassiz's "Essay on Classification," published in 1857, I was astonished to find what stress he placed on the study of the "habits of animals," as he put it.

"Without a thorough knowledge of the habits of animals," he said, "it will never be possible to determine what species are and what not." Today we would call this a biological species concept. He goes on to say that we want to find out "how far animals related by their structure are similar in their habits, and how far these habits are the expression of their structure." He continues, "How interesting would be a comparative study of the mode of life of closely allied species." Indeed, Agassiz proposes a program of study which is virtually identical with that of the founders of ethology more than 50 years later: "The more I learn about the resemblances between species of the same genus and of the same family . . . the more am I struck with the similarity in the very movements, the general habits, and even in the intonation of the voices of animals belonging to the same family . . . a minute study of these habits, of these movements, of the voice of animals cannot fail, therefore, to throw additional light upon their affinities."

An interest in the behavior of animals is still a tradition in the MCZ, more than 100 years later. Half of my Ph.D. students in the last 20 years, for example, did their theses on problems of behavior. One of the outstanding characteristics of the so-called new systematics is the concern with the attributes of the living animal. Variation, adaptation, speciation, and evolutionary change cannot be fully understood unless the field work is supplemented by experimental research in population genetics, the analysis of protein and chromosomal variation in populations, the study of the relations between adaptation and functional morphology, to give merely a few examples. Laboratories for such studies are a major component of the new wing. Environmental physiology, another aspect of animal adaptation of great interest to the evolutionist, is being studied at the Countway Laboratories of the Concord Field Station.

The outside world has been largely oblivious to these developments and, I am sorry to say, unfortunately so have also many systematists. For the modern systematist, however, all this seems to be a perfectly natural development. Anyone who has read books like Huxley's *New Systematics* (1940) or my own *Systematics and the Origin of Species* (1942) knows to what an extent all these mentioned activities have been part of systematics for at least 30 years. The new wing gives us an opportunity to help correct the false image about museums which is still widely held, and replace it by the new concept, the beginnings of which were already outlined by Louis Agassiz 116 years ago.

The new wing signals to the outside world that the MCZ is not merely a repository of collections but a biological research institute that differs from the other laboratories in the Biological Laboratories only in the nature of the subject matter. While the emphasis in much of the Biological Laboratories is on cells and the molecular constituents of cells, the major emphasis in the MCZ is on the whole organism, on the diversity of organisms and on their evolution. Since closest contact between the two groups of investigators is of the utmost mutual benefit to both of them, the organization of the Department of Biology was modified in recent years in order to integrate the staffs of the two groups. Research and teaching are the objectives of both of them.

In this day and age science is no longer conducted merely for its own sake. Science is no longer the tenant of an ivory-tower.

Without wanting to minimize in any way the indispensability of basic science, we now realize that the scientist also has social obligations. When optimistically inclined he will say that he is helping to build a better world; when pessimistically inclined he will say he is trying to prevent a further deterioration of this world.

But he cannot do this unless he has a sound understanding of Man and of the world in which he lives. And it is precisely the study of diversity and of evolutionary history which has made a major contribution toward the development of a *new image of Man.*

In the pre-Darwinian literature, and also, in much of certain types of contemporary literature, man is conceived as a static being, created within an equally static nature that is subservient to him. Ever since Darwin this concept has increasingly been replaced by a new image, an image of an evolved and still evolving man, part of the evolutionary stream of the whole living world. And this new image, the direct product of evolutionary and natural history studies, is of critical importance, not only for our personal concept of the world in which we live, but also for such quite practical issues as man's relation to the environment, to the natural resources, and indeed even to the interaction among men.

It is about time we realize that the future of mankind is not something "written in the stars," something controlled by external forces, but that it is we humans ourselves who hold the fate of our species in our hands. We now have a fairly good idea what the major ills of mankind are and it has become quite clear that only a few of them are susceptible to purely technological solutions. Instead, most of them are of a behavioral-sociological nature and require a change in our value systems, a change one is not likely to accept unless one has a far better understanding of nature, of the dynamics of populations, of the biological basis of behavior, and of other components of the biology of organisms, than most of those have who are responsible for policy decisions.

It will require a deeper understanding of the mentioned problems and it will require massive education based on the findings that emerge from the type of researches that we are planning. During the planning of the wing we sometimes referred to it as a new "center for environmental and behavioral biology." Although this title was not officially adopted, it is indeed an apt description of the focus of attention of the investigators in our new facility.

There may be some who have not kept up with recent developments in biology and who might consider it far-fetched to claim that the mentioned problems fall within the area of interest of systematics. And yet with systematics defined as the science of biological diversity and with the organism defined as something living and not merely a preserved specimen, a solid chain of links is formed from the systematics of Linnaeus through that of a Louis Agassiz to that of the modern evolutionary systematist and population biologist.

I add my vote of thanks to those who have made the creation of this new center of environmental and behavioral biology possible. I predict that it will have an impact on our knowledge and our thinking that will reach to the far corners of the earth.

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A NEW SPECIES OF *CYRTODACTYLUS* (GECKONIDAE) FROM NEW GUINEA WITH A KEY TO SPECIES FROM THE ISLAND

Walter C. Brown[1]
and
Fred Parker[2]

Abstract. A new species of *Cyrtodactylus* from New Guinea is described. The type locality is Derongo at an altitude of 1300 feet on the Alice River tributary system to the upper Fly River, in western Papua, New Guinea. A key to the species of *Cyrtodactylus* which have been recorded from New Guinea is also provided (see de Rooij, 1915, for descriptions of most of the species).

Introduction

Of the nine species of *Cyrtodactylus* previously recorded from New Guinea, known ranges of at least two (*C. sermowaiensis* and *vankampeni*) are restricted to one or two localities. The species described in the present paper may also exhibit a limited range, for although the junior author has collected extensively in papuan New Guinea for several years, no specimens have been collected thus far outside of the type locality in the headwaters of the Fly River.

Inger (1958) calls attention to the usefulness of the pattern of the enlarged scales in the preanal region and on the under surface of the thighs as characteristics for distinguishing species of *Cyrtodactylus,* and uses it in the key to the species from the Philippines and Borneo. We have found these characters similarly useful in separating most of the New Guinea species. We have not had the opportunity to examine specimens of *C. novaeguineae.*

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Cyrtodactylus derongo new species

Holotype. Museum of Comparative Zoology R126205, an adult female, collected by Fred Parker in the Derongo area at an elevation of 1300 feet, Alice River system, tributary to the upper Fly River, Papua, New Guinea, 8 April 1969.

Paratypes. Museum of Comparative Zoology R126203, 126204, and 126206, Papua New Guinea Museum R995, and American Museum of Natural History 103910, same data as the holotype.

Diagnosis. A *Cyrtodactylus* with small scales on posteroventral surface of thighs meeting the enlarged scales of anteroventral surface at a sharp boundary; the rows of enlarged femoral scales forming a continuous series with preanal rows; enlarged preanal scales posterior to the pore series absent; dorsal ground color dark brown with very faint darker blotches enclosing irregular rows of large, white tubercles (Fig. 1).

Description. A moderately large *Cyrtodactylus;* four adult females measure 105–112 mm snout–vent length, one specimen 81 mm in snout–vent length is immature; head about one and one-half times its breadth; eye, large, its diameter about one-third of the length of the head and about equal to its distance from the nostril; diameter of ear opening less than half its distance from the eye; head covered with granules, very small posteriorly and somewhat larger anteriorly; scattered, moderate-sized, pointed tubercles as far anterior as the interorbital region; rostral large, rectangular, its breadth about 60 percent of its length, nostril bordered by the rostral, supranasal, first labial and 3 small shields; upper labials 11 or 12; lower labials 11 to 13; supranasals large, separated by 1 or 2 scales; one large pair of postmentals in contact posteriorly for about half their length; distinct lateral fold lacking, but its normal position marked by a row of flattish tubercles separated from one another by several smaller scales; in the mid-body region, 20 irregular lines of dorsal tubercles between the aforementioned rows of flattish scales; 15 to 18 rows in the axillary region; some of the tubercles are white and tend to form widely separated irregular transverse lines, 8 to 10 between the nape and the hind limbs; undersurface of

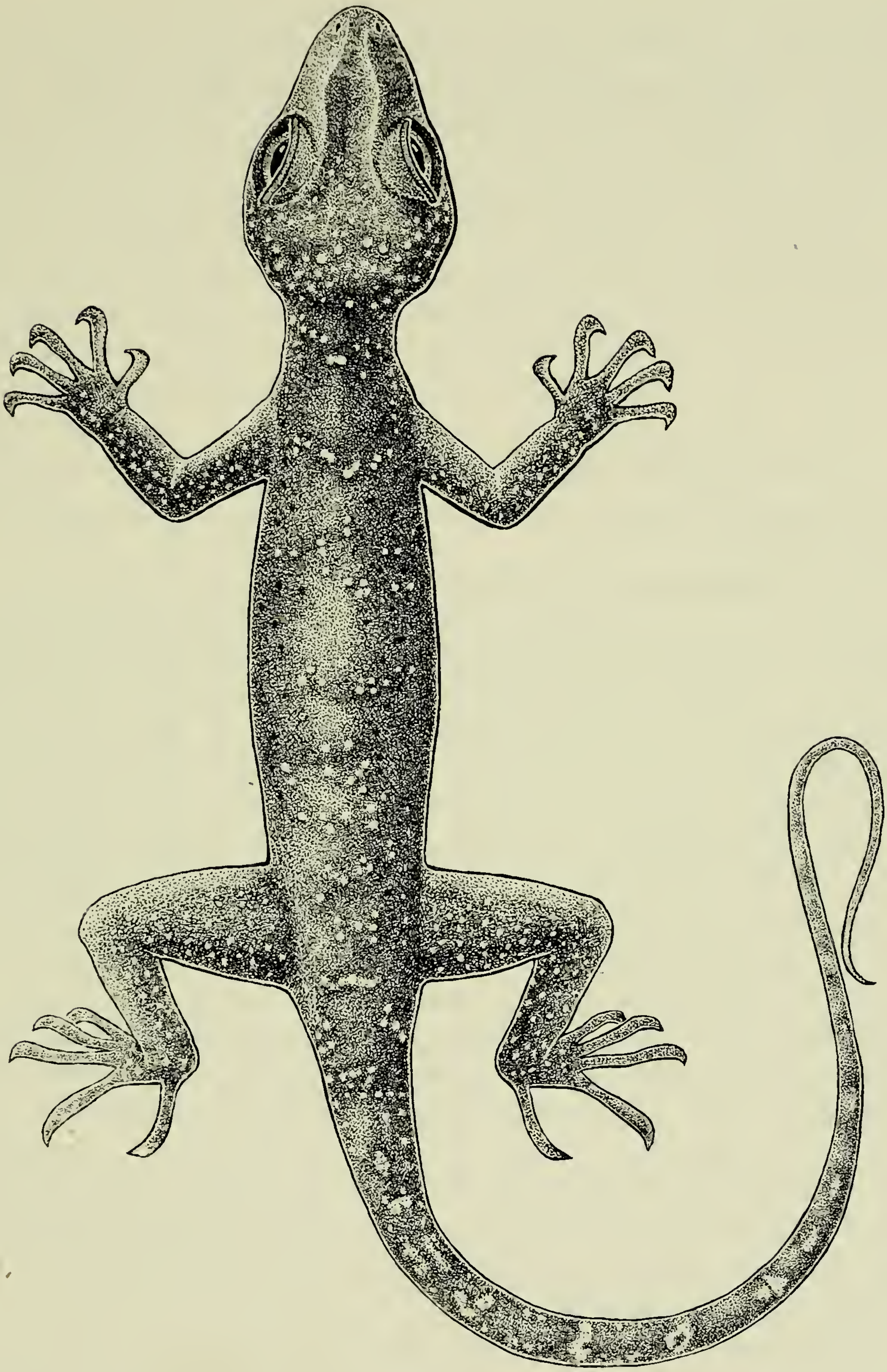

Figure 1. Dorsal view of *Cyrtodactylus derongo,* MCZ 126205, type specimen.

head with small granules; venter with about 46 to 48 rows of scales at the mid-body between the ventrolateral rows of tubercles, small and granular laterally, but merging gradually with the large cycloid scales of the mid-venter; the large preanal-pore scales in a very shallow "/\" continuous with a row of femoral-pore scales that are gradually reduced in size along the femur; those anterior to the pore row somewhat enlarged, flattish scales on both the thighs and the preanal region, the latter merging with those of the venter; posteriorly the pore series is met abruptly by small granular scales in both the preanal and femoral regions; 24 to 26 rows of lamellae and scales beneath the fourth toe; tail only slightly depressed, with square or rectangular plates toe; tail only slightly depressed, with square or rectangular plates on the ventral surface and with every fourth or fifth scale distinctly enlarged.

Snout–vent length of holotype 105 mm.

Color (*in preservative*). The dorsum is dark reddish brown with 9 or 10 very faint series of darker blotches each enclosing two to several large white tubercles; the latter tend to form very irregular, widely separated, transverse rows; in the intervening areas the tubercles are dark or have a faint whitish tip; scattered white tubercles also occur on the posterior part of the head, the dorsal surfaces of the limbs and the base of the tail; venter lighter brown, most dilute on the head and throat, each scale marked by a varying number of small brown spots and flecks. In life, the dorsal ground color is dark purplish brown; the venter is paler and more translucent. The iris is deep brown.

Habitat note. The specimens of *Cyrtodactylus derongo* were collected from crannies and hollows in trees in dense rain forest. Natives state the species is completely arboreal. Two other species of *Cyrtodactylus, papuensis* and *mimikanus,* are sympatric with *derongo,* and were observed both on the forest floor and on trees a few feet above the ground. A possible fourth species, also arboreal, was observed in the same area but specimens are not available for identification.

Comparisons. Differs from other Indo-Australian species of *Cyrtodactylus* in the rather uniformly dark ground color of dorsum marked by large white tubercles. The color pattern is reminiscent of that of *Underwoodisaurus milli,* but in the latter the white patches involve small surrounding scales, and the patches may be fused into partial or complete transverse bands. Compared to other New Guinean species, *C. derongo* is somewhat intermediate in size along with *mimikanus, marmoratus, papuensis,* and *pelagicus,* and in contrast to the diminutive *vankampeni* and the larger *loriae, louisiadensis* and *novaeguineae.* It also differs from other species, with the possible exception of *novaeguineae* (not examined), in the pattern of enlarged preanal and femoral scales, and in lacking enlarged scales posterior to the pore series in the preanal area. *C. pelagicus* and *vankampeni* exhibit no or only very slightly enlarged scales in the pore series; *loriae, louisiadensis, mimikanus, marmoratus,* and *papuensis* exhibit 3 to 8 or 9 short rows of large scales posterior to the pore series in the preanal area.

KEY TO *Cyrtodactylus* FROM NEW GUINEA

1. a. Preanal region, or both preanal and femoral regions, with one or more rows of distinctly enlarged scales. 3
   b. Preanal and femoral regions covered by relatively uniform small scales, even the pore series not distinctly enlarged. 2
2. a. Dorsal rows of tubercles at mid-body 22–24, usually 10 at region of fore limbs; 8–12 preanal pores, femoral pores absent. .... *pelagicus*
   b. Dorsal rows of tubercles at mid-body 10–12, usually 6 at region of fore limbs; 45–50 preanal and femoral pores in a continuous series. .... *vankampeni*
3. a. Dorsum usually marked by a pattern of light and dark bands or distinct dark blotches of varying size; or if melanistic, lacking prominent, white tubercles. 4
   b. Dorsum dark brown with very faint darker blotches enclosing prominent, white tubercles, which tend to form narrow, irregular, partial or complete transverse series; a continuous series of preanal and femoral pore scales (females) preceded anteriorly by several rows of enlarged scales, those in the preanal region merging with those of the venter; no enlarged scales posterior to the pore series in the preanal region .... *derongo*
4. a. One or more rows of enlarged femoral scales; upper labials usually not greater than 12. 5
   b. No enlarged femoral scales; 12–14 upper labials; 10–11 broad lamellae under basal portion of fourth toe; dorsum with a double or united series of 5 or 6 rather large dark blotches between ear region and base of tail, separated by light bands variably marked by 3 or 4 smaller dark blotches; males without pores. .... *sermowaiensis*
5. a. Enlarged preanal pore scales in a shallow "/\" chevron. 7
   b. Enlarged preanal pore scales compressed into a narrow "/\" sunk in a groove in males with 8–14 pores. 6
6. a. Seven to 9 moderately narrow, dark, irregularly margined bands or series of blotches between the ear region and the groin; 8–10 preanal

pore scales bearing pores in males, preceded anteriorly by 1 or 2 rows of much enlarged scales and followed posteriorly by a narrow cluster of 8–12 enlarged preanal scales; preanal series widely separated from a single row of much enlarged femoral scales; no femoral pores. .... *papuensis*

b. Seven to 9 irregularly margined, dark bands or blotches between the ear region and the groin; 12–14 preanal pore scales bearing pores in males, preceded anteriorly by several rows of enlarged scales merging with those of the venter and followed posteriorly by several rows of enlarged scales which diminish gradually; several rows of enlarged femoral scales continuous with the enlarged preanal series; a short series of 4–6 femoral pores separated from the preanal series. .... *marmoratus*

7. a. Dorsum with five broad, dark, rather even-margined, transverse bands or double series of blotches between the ear region and the groin; 26–28 irregular rows of rather small, unikeeled tubercles between lateral folds at mid-body; a continuous series of enlarged preanal and femoral pore scales bearing 38–80 pores[1] for several males examined but in each instance reaching the distal end of the femur, both preceded anteriorly by several rows of enlarged scales merging with those of the venter in the preanal region, followed posteriorly by several rows of enlarged preanal scales that diminish gradually. .... *louisiadensis*

b. Dorsum with 5 to 8 broad to narrow dark bands or series of blotches, usually with irregular margins, between the ear region and the groin; 20–22 irregular rows of tubercles between lateral folds at mid-body; a continuous or interrupted series of preanal and femoral pore scales, some bearing pores in males. 8

8. a. Dorsum with 5 dark transverse bands or series of blotches between the ear region and the groin; males with a continuous series of preanal and femoral pores. 9

b. Dorsum with 7 or 8 dark transverse bands or series of blotches between the ear region and the groin; a series of enlarged preanal scales bearing 12–14 pores in males; often separated by 3 or 4 somewhat smaller scales from the pore-bearing femoral series; in males the latter bearing a median group of 0–5 pores and a distal group about 5–11 pores on either side; both preanal and femoral series preceded anteriorly by several rows of enlarged scales which in the body region merge with those of the venter; and in the preanal region also followed posteriorly by several rows of enlarged scales which gradually diminish in size. .... *mimikanus*

9. a. A continuous series of preanal and femoral pores extending the length of the femur, bearing in males an uninterrupted series of 60–70 preanal and femoral pores; preanal pore series preceded by several rows of enlarged scales merging with those of the venter, and followed posteriorly by 3 or 4 rows of enlarged scales; femoral scales anterior to the pore series exhibiting a gradual reduction in number of scales and a resultant strongly tapered appearance; 20–24 lamellae and enlarged scales beneath the fourth toe; small, roundish tubercles absent from throat. .... *loriae*

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[1] This wide range may reflect population differences, since in our small sample those with the lowest number of pores were from Australia and those with the largest number from the Solomon Islands.

b. A series of enlarged preanal and femoral pore scales, bearing a continuous series of 38–42 preanal and femoral pores in males; 28–33 lamellae and enlarged scales under the fourth toe; throat with some scattered small rounded tubercles (from description by Brongersma, 1934) . ... *novaeguineae*

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MORPHOGENESIS, VASCULARIZATION AND PHYLOGENY IN ANGIOSPERMS[1, 2]

G. LEDYARD STEBBINS[3]

ABSTRACT. Evidence is reviewed to support the hypothesis that vascular strands in the angiosperm flower which some botanists have regarded as "vestigial" can be understood better if they are regarded as the result of irregularities in development, which provides no indication with respect to the alternatives of phylogenetic reduction vs. amplification. Nevertheless, the concept of the conservatism of vascular anatomy is supported by the probability that genes acting late in development can more easily give rise to mutations that can become incorporated into a harmonious genotype than can genes that act early in development. Examples from the development of achenes in various genera of the family Compositae show that size of mature achene is not necessarily correlated with complexity of vascular anatomy, and that this anatomy may reflect the particular course of development, particularly the time when procambial initials are differentiated. In this family, genera that are generally regarded as more closely related to each other tend to have more similar developmental patterns than those that are more distantly related.

Ever since the 19th-century research of Celakovsky (1896), botanists have asked the question: "Is the arrangement of vascular bundles in the organs of higher plants a more reliable guide than outward form to homology and the direction of evolution?" Until very recently, the usual answer has been affirmative (Eames, 1931, 1961; Puri, 1951, 1952; Melville, 1962), al-

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[1] Much of the material in this paper is reproduced from the author's book: *Flowering Plant Evolution Above the Species Level,* Harvard University Press (in preparation), through kind permission of the Press.

[2] This paper is respectfully dedicated to my former teacher and mentor, Ralph H. Wetmore, who was largely responsible for developing my interest in comparative plant anatomy.

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though botanists have differed widely with respect to interpretations of anatomical structure. In particular, single vascular bundles that appear to have no function have been designated as "vestigial." They have been interpreted as vestiges of organs that are no longer formed, and therefore as indicating widespread, predominant trends of reduction. Furthermore, the concept of "fusion" has been adopted to interpret situations in which two related species or genera differ with respect to the number of parallel bundles found in an organ. If a form has two parallel bundles in a particular position, it is regarded as more generalized or primitive than a related form that has only one bundle in that position.

During the last decade, botanists have become increasingly skeptical of such notions. An extreme form of this skepticism has been expressed by Carlquist (1969). After an extensive review of the entire problem, he reaches the following conclusion (p. 334): "Anatomy of flowers can be studied meaningfully only in relation to adaptations for particular modes of pollination, dispersal and allied functions."

In my opinion, neither the rigid interpretations of Eames, Puri, Melville and their followers nor the complete skepticism of Carlquist are justified. Later in this article, examples are given to show that when comparing even such similar and certainly homologous structures as the achenes of different Compositae, one finds many exceptions to a supposed correlation between organ size and complexity of vascularization. On the other hand, several examples exist in the literature to show that supposed "vestigial bundles" can be associated with either increase or decrease in numbers of parts. One of the clearest of these was presented long ago by Murbeck (1914). In two species belonging to the family Rosaceae, *Comarum palustre* and *Alchemilla vulgaris* (sens. lat.), he found rare deviations from the normal or modal number of calyx lobes, in both an upward and a downward direction. In *Alchemilla,* for instance (Fig. 1), the normal number of lobes is four, but occasional flowers have three lobes and others have five. Most important, however, is the fact that among 3-lobed as well as among 4-lobed calyces are examples in which one of the lobes is larger, and may have a double-pointed apex, as well as extra vascular bundles. According to the classical interpretation, such 3-lobed calyces result from a trend of reduction via "fusion," and the extra bundles found in the larger lobe are "vestigial." If, however, this interpretation

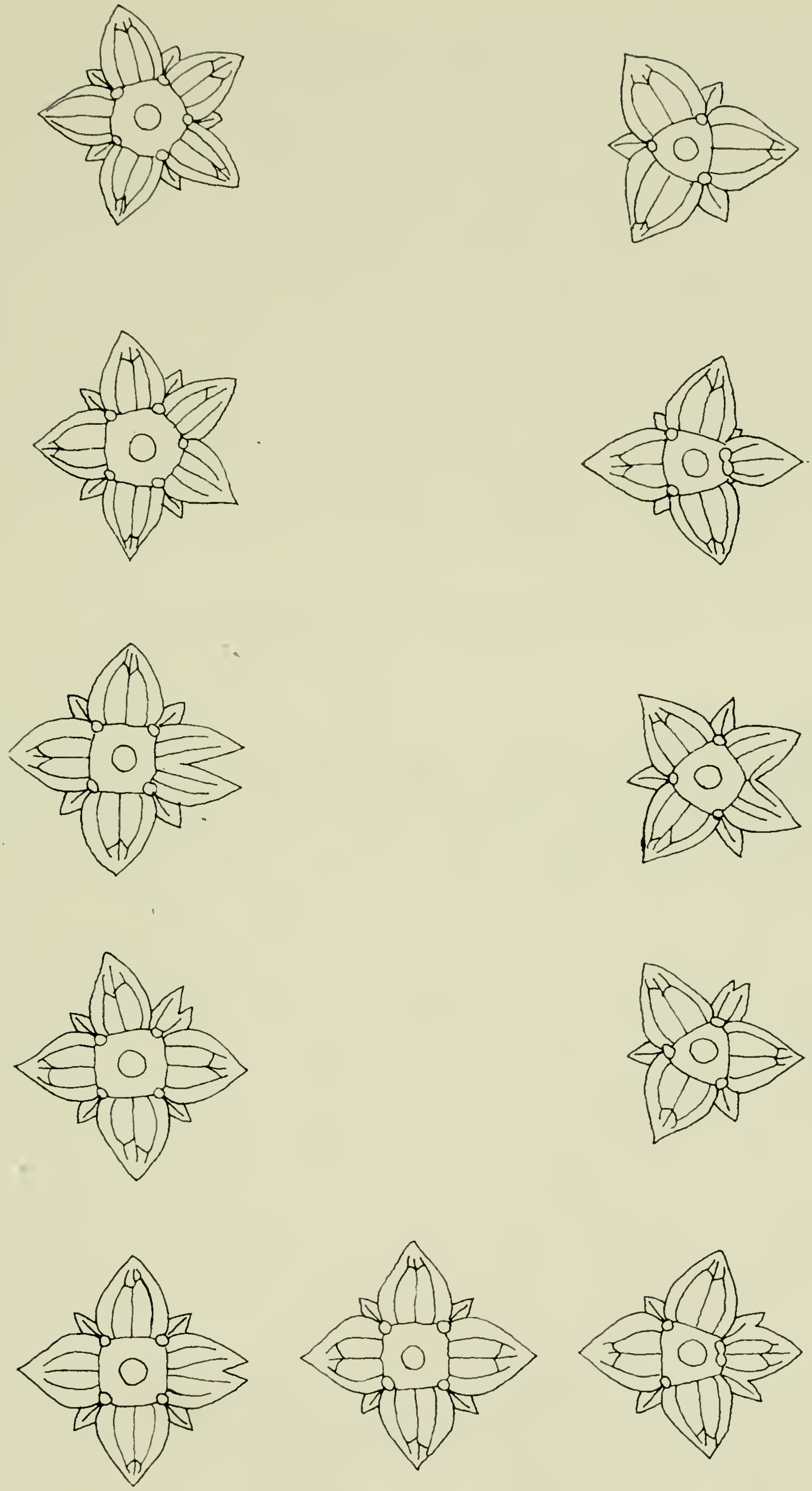

Figure 1. Calyces of individuals of *Alchemilla vulgaris,* showing deviations from the normal 4-merous condition in the direction of both decrease and increase in lobe number, as well as intermediate situations with abnormal lobe number and structure. From Murbeck, 1914.

is to be consistent, the larger lobes of the aberrant 4-lobed calyces would have to be interpreted in the same way, and the conclusion would have to be reached that the basic number of calyx lobes in *Alchemilla vulgaris* is five rather than four. Such an interpretation is contradicted by the fact that 4-merous calyces are found throughout the genus *Alchemilla,* except for rare aberrant individuals like those described by Murbeck. In *Comarum palustre,* similar aberrant calyces have five lobes, one of which is larger than the others and contains extra vascular bundles. If one held strictly to the concept of reduction and vestigial bundles, one would have to interpret these calyces as indicating that the calyx of *Comarum* was originally hexamerous. Since hexamerous calyces are almost completely lacking, not only in the family Rosaceae but also in the entire order Rosales, such an interpretation is absurd.

A Morphogenetic Intrepretation of “Vestigial Bundles”

These examples are best interpreted by discarding entirely the concept of reduction and vestigial bundles, as well as any other phylogenetic concept, and regarding them entirely in the light of developmental genetics. The aberrant calyces found by Murbeck are comparable to the aberrant corollas described by Huether (1968) in *Linanthus androsaceus,* and shown by him to represent unusual gene combinations that render the plant more susceptible than normal individuals to producing aberrant phenotypes, or phenodeviants, as a result of normal environmental fluctuations during development. Deviations from the normal or modal condition can occur in either direction. Using a developmental approach, they can be explained on the basis of a formula that I suggested a few years ago (Stebbins, 1967). The number of similar organs or parts that are produced in a particular whorl can be represented by the quotient $A^n + \frac{a^m}{a^i}$, where A^n is the final number of parts, a^m is the total number of meristematic cells that are capable of producing an A-type part, and a^i is the number of meristematic cell initials needed to produce a single A-type part.

Applying this formula to Murbeck's examples, one could suggest that in the normal development of the calyx of *Alchemilla,* the relation of a^m to a^i is on the order of 20 to 5, so that $A^n = 4$.

In the extreme aberrants, a^i remains the same, but a^n has become respectively 15 and 25. On the other hand, 3-lobed calyces of which one lobe is larger and has extra bundles would result from values such as $a^m = 17$ and $a^i = 5$, so that $A^n = 3.4$. Similarly, abnormal 4-lobed calyces would represent the quotient $A^n = 4.4$, resulting from values of $A^m = 22$ and $a^i = 5$.

Morphogenetic evidence with respect to "vestigial" bundles in the androecium of various species belonging to the order Malvales has been obtained by van Heel (1966). He showed that in several instances vascular bundles, which in the mature flower were not associated with any recognizable structure, nevertheless appeared in a position where small stamen primordia could be recognized in early stages of development. These primordia later became enveloped by the growth of the surrounding tissue, presumably produced by persistent intercalary meristems. These examples could be regarded either as terminal stages of a reduction series, or intermediate stages of a trend toward amplification.

The most convincing evidence regarding the morphogenetic significance of vascularization comes, however, from experiments in which the conditions under which vascular tissue appears have been determined, or have been altered in specific ways. Only two such experiments are known to me. One of them, by Wetmore and Rier (1963), showed that vascular tissue arises in callus tissue at positions that are at regular distances from each other, and that their distributional pattern can be altered as a result of relatively slight alterations in the nutritive medium. Consequently, the appearance of a bundle in an unexpected position requires only a slight shift in the distribution of nutritional factors or in the balance of hormonal interactions within the developing system.

In the other experiment, Torrey (1955, 1957) altered experimentally the number of protoxylem points in a pea root. He found that when 0.5 mm of the distal portion of the root, containing only cells that are not visibly differentiated, was isolated and cultured *in vitro*, the great majority of cultures produced roots having the normal triarch condition. About 2 percent of the cultures, however, which were tips of relatively small size, produced at first diarch roots, which later reverted to the triarch condition.

If to the culture he added indole acetic acid at a concentration of 10^{-5} molar, he obtained a greater proliferation of the cells from which vascular tissues are differentiated. As a result, he converted the triarch to the hexarch condition, and found that the latter condition persisted indefinitely. The number of protoxylem points could, therefore, be increased or decreased, depending upon the amount of meristem present when procambial differentiation took place.

These two experiments suggest that much can be learned about the processes that affect the pattern of vascularization by various kinds of experimental approach. This is a field of morphogenesis that has not yet been well developed but that promises eventually to provide a bridge over which visible changes in vascular anatomy can be related to specific alterations of the genotype, as they affect developmental processes.

Vestigial Characters in Plants and Animals

The results just reviewed suggest that with respect to any group of similar structures, such as parts of a perianth, stamens in an androecium, or "carpels" in a gynoecium, evolutionary change can involve either increase or decrease in number, and that the anatomical features associated with either trend are similar to each other. Vascular anatomy cannot tell us whether or not the ancestors of a particular form had more or fewer sepals, petals, stamens, or carpels.

The belief of plant anatomists that this is possible rests, in my opinion, on a mistaken analogy with the genuine vestigial structures found in animals. These latter, such as the gill slits of the vertebrate embryo and the vermiform appendix, have a complex and distinctive developmental pattern. The so-called "vestigial bundles," on the other hand, are identical in structure with the bundles that are unquestionably functional. Furthermore, the procambial cells that form the xylem and phloem of these bundles are probably differentiated from meristematic cells during a single mitotic cycle (Olson *et al.,* 1969). More important, the epigenetic sequence responsible for the formation of these bundles is an exact repetition of a course of events that occurs in many other parts of the plant; only the position where it occurs is distinctive.

A Developmental Hypothesis That Favors Conservatism of Vascular Anatomy

The concept of vestigial bundles is part of a broader concept that views vascular anatomy as more conservative than external morphology. This concept has been rejected by Carlquist (1969) as an "insufficient and fallacious framework on which most phylogenetic interpretations of floral anatomy still rest." He nevertheless concedes that degree of union between vascular bundles can be "conservative." Is there any logic to this acceptance of a part of the doctrine of conservatism, after most of it has been rejected?

I believe that botanists must examine the problem from the viewpoint of developmental genetics and morphogenesis, since this brings us closer to the basic nature of evolutionary changes. When we do this, we can recognize and emphasize the fact that the procambial initials from which vascular bundles arise become differentiated from the ground meristem at a very early stage of the development of primordia. Consequently, alterations of vascular pattern require changes in the time of action of genes that normally act very early in development. Alterations in the action of genes that normally act at later developmental stages can produce changes in size or form without altering the pattern of vascularization.

Is there any logical reason for assuming that genes which produce their effects at early stages of development are less likely to play a role in evolutionary change than genes which affect later stages? A positive answer to this question is the genetic basis for recognizing Von Baer's principle of embryonic similarity, which was used by Darwin (1872) as embryological evidence for evolution, and has been applied more recently to animal development by De Beer (1951), and to plants by the present author (Stebbins, 1950). The reasoning is as follows. Adult characteristics are assumed to be the products of epigenetic sequences of gene action in development, so that later processes depend in part upon the nature of gene products produced at earlier developmental stages. Moreover, the action of most genes is pleiotropic in the sense that their primary products may have many secondary effects. The earlier is this primary action, the greater is the amount of pleiotropy that is possible, and the more widespread are the secondary effects of genes. Hence mutations of genes affecting early stages are more likely to produce profound alterations of development, and hence to upset the entire developmental system, than are mutations of late-acting genes. The milder alterations produced by these latter mutations are more likely to adjust the individual in a harmonious fashion to new selective pressures than are the more drastic effects produced by mutations of genes that act early in development. Hence, adaptive alterations of morphology are brought about more often by late-acting genes than by those acting early in development. In other words, genes acting early in development tend to be conservative with respect to the establishment of their mutations in populations. Among such genes are those that affect the differentiation of procambial strands.

Relationships Between Organ Size and Amount of Vascularization

In the remainder of this contribution, I would like to apply the theoretical concept just developed to two situations. The first is the relationship between organ size and amount of vascularization. If vascularization is related only to adaptation and physiological function, as Carlquist has assumed, then large organs should always have a proportionately greater amount of vascularization than homologous, smaller ones. On the other hand, if preferential establishment of late-acting gene changes is a significant factor, then the relationship between size and vascularization would have a historical or evolutionary component.

Among homologous organs having approximately the same size, but different patterns of vascularization, one might postulate that the one having the more complex pattern resembles most closely the most primitive organ of the group in question, while the simpler pattern has been derived by a process of reduction that affected early stages of development, followed by a reversal of evolutionary direction, in which increase in size was accomplished by establishment of genes acting late in development. Similarly, in comparisons between homologous organs of very different sizes, but having similar, relatively simple patterns of vascularization, one might postulate that the smaller organ more nearly resembles a reduced, ancestral form, and the larger one has been derived via secondary enlargement.

Ovary and Achene Development in the Family Compositae

A good object for testing these hypotheses is the ovary and achene in the family Compositae. In different genera of this

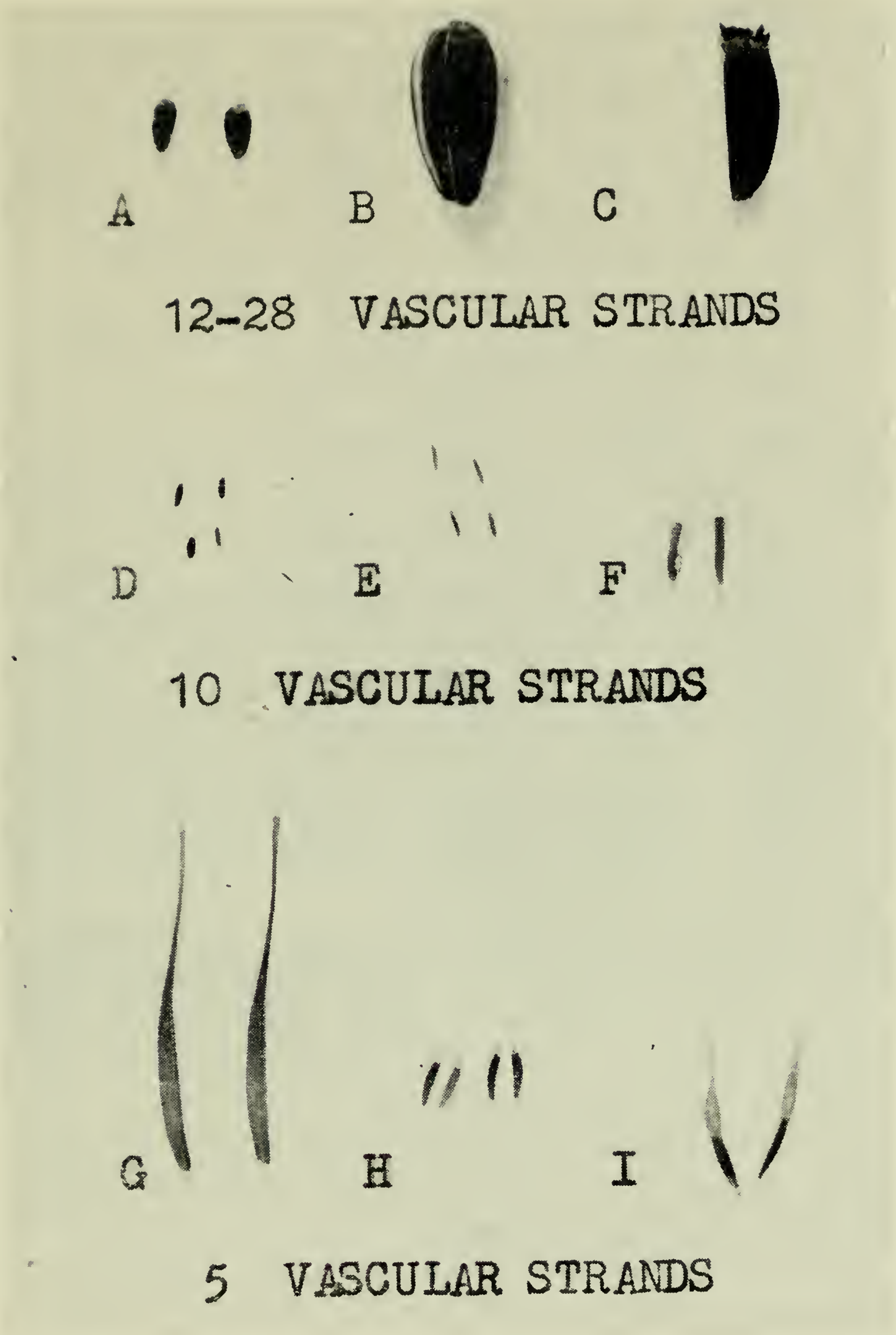

Figure 2. Mature achenes of various species of Compositae of which the development is recorded in Tables 1 and 2. A, *Helianthus annuus,* wild form from east of Davis, Calif. B, *Helianthus annuus,* cultivated variety from Department of Agronomy, University of California, Davis. C, *Wyethia glabra,* from Cache Creek Canyon, Yolo County, Calif. D, *Senecio cruentus,* cult. var. *"stellata"* (smaller heads). E, *Senecio vulgaris,* from campus, University of California, Davis. F, *Microseris nutans,* from Wright's Lake, Eldorado County, Calif. G, *Tragopogon porrifolius,* from Locke, Sacramento County, Calif. H, *Stephanomeria exigua* ssp. *coronaria,* from Antioch, Calif. I, *Microseris douglasii,* from south of Dixon, Solano County, Calif.

family, an enormous range of size exists between mature achenes having a length of 1.4 mm to achenes 20 times as long, and many-fold greater in bulk (Fig. 2). With respect to anatomy, the most complex patterns consist of 26 to 28 parallel bundles traversing the ovary and achene (Stebbins, 1940), while in the simplest ones, only two bundles are present (Stebbins, 1937). The poor correlation between size and complexity of vascularization is shown in Figure 2, which illustrates the mature achenes of ten forms belonging to this family. In three of these (A–C), the ovary and achene are traversed by 12 to 28 parallel vascular strands, while in the remaining three (G–J) only five are present. In the first group, achene length ranges from 2.92 mm to 13.65 mm; in the second, from 1.4 mm to 5 mm; and in the third, from 3.8 mm to 28.5 mm. I admit that the largest example of the latter group, *Tragopogon porrifolius,* was chosen to represent an extreme example of large size associated with a relatively simple vascular pattern, so that one cannot conclude from this tiny sample that an inverse correlation exists between achene size and amount of vascularization. Nevertheless, the lack of a significant positive correlation in the family as a whole seems to me highly probable on the basis of my acquaintance with a large number of genera.

In order to discover more about the relationships between vascularization and developmental patterns, I have compared the ovaries of these species at four stages of development: (1) the smallest size at which procambial strands can be recognized; (2) the first appearance of xylem tracheids; (3) anthesis; and (4) mature achenes. Since the Composite achene increases far more in length than in width, mean length of the ovary at each of these stages is a reliable indicator of overall size. The stages were determined both from sectioned material and from whole mounts cleared according to the schedule of Herr (1971) and observed under Nomarski interference-contrast optics.

Preliminary results of this study are shown in Tables 1 and 2. Table 1 gives the mean lengths of the ovary and achene at four different stages: differentiation of procambium; first differentiation of xylem strands, anthesis, and seed maturity. The final column of this table gives the mean number of vascular strands in the ovary at anthesis. Table 2 presents the mean percentage growth increment for each interval between the stages listed in Table 1. To obtain these values, the difference between the length at a later stage and at the next earlier stage,

Table 1. Lengths of ovaries and achenes of some species and varieties of Compositae at selected stages.

Species or variety	Procambial differentiation (P)	Xylem differentiation (X)	Anthesis (A)	Maturity (M)	Xylem strands at anthesis
Wyethia glabra	0.253mm	0.631mm	11.25mm	13.65mm	12–17
Helianthus bolanderi ssp. exilis	0.198	0.291	2.01	2.92	19–21
Helianthus annuus wild (near Davis, Cal.)	0.251	0.38	1.596	5.52	18–24
Helianthus annuus cultivated	0.208	0.442	9.90	13.65	26–28
Senecio cruentus cult. small heads	0.234	0.732	0.868	1.43	10
Senecio cruentus cult. large heads	0.228	0.61	1.41	1.66	10
Senecio vulgaris	0.186	0.772	1.135	2.35	10
Microseris nutans	0.294	0.997	1.366	5.04	10
Microseris douglasii	0.194	0.999	1.67	4.96	5
Stephanomeria exigua	0.205	0.524	1.449	3.86	5
Tragopogon porrifolius	0.242	0.934	1.912	28.5	5

Table 2. Proportional growth increments at successive stages of ovaries of Compositae. Symbols explained in Table 1, and in text.

Species or variety	$\frac{X-P}{P}$	$\frac{A-X}{X}$	$\frac{M-A}{A}$
Wyethia glabra	1.49	16.8	0.23
Helianthus bolanderi ssp. exilis	0.47	5.91	0.45
Helianthus annuus wild	0.51	3.20	2.46
Helianthus annuus cultivated	1.12	21.40	0.38
Senecio cruentus cult. small heads	2.12	0.17	0.65
Senecio cruentus cult. large heads	1.70	1.31	0.18
Senecio vulgaris	3.10	0.47	1.07
Microseris nutans	2.39	0.37	2.69
Microseris douglassi	4.15	0.67	1.97
Stephanomeria exigua	1.56	1.77	1.66
Tragopogon porrifolius	2.85	1.05	13.91

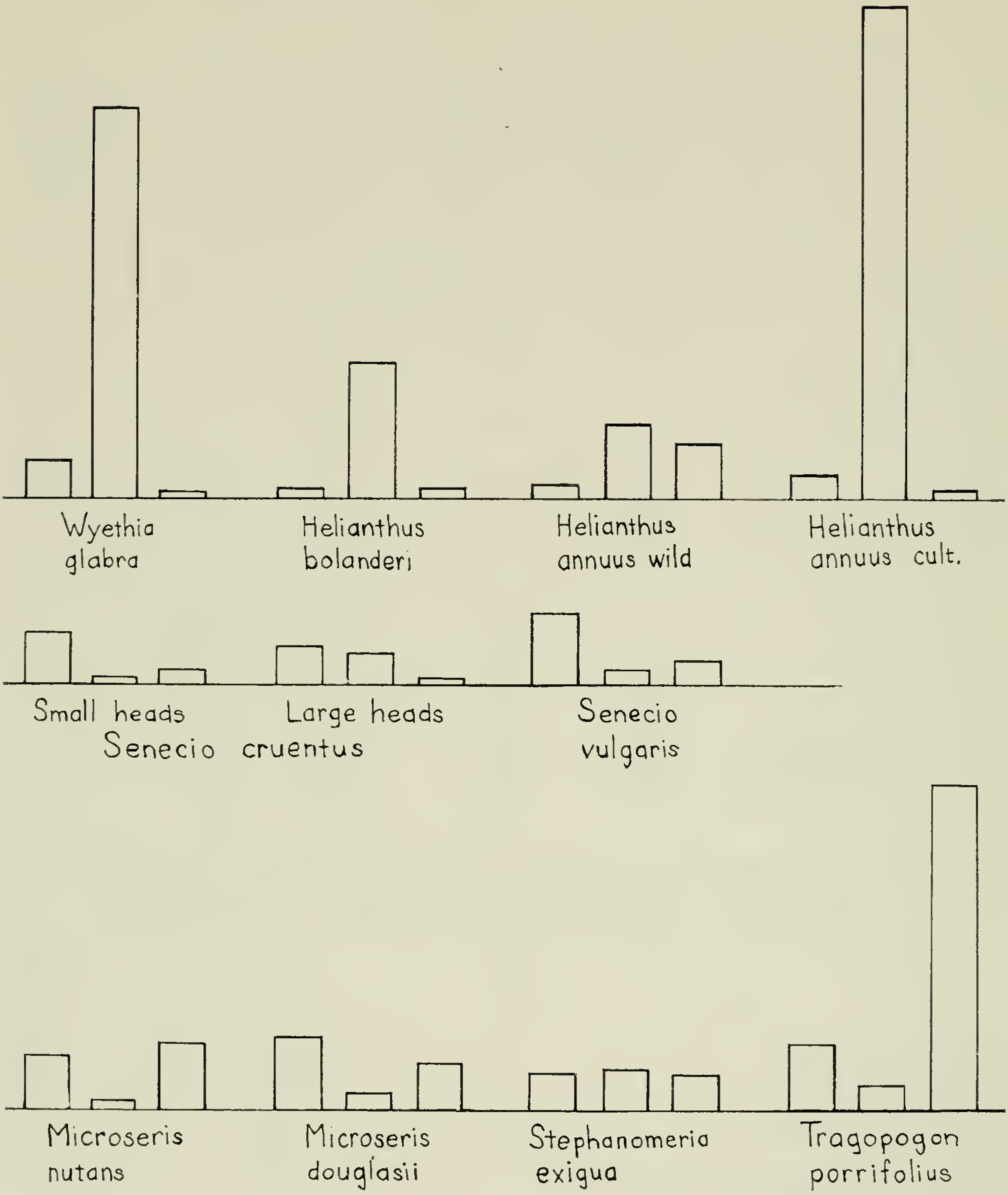

Figure 3. Chart showing diagramatically the growth increments of ovaries of Compositae, as recorded in Table 2.

i.e., the amount of growth during the interval, is divided by the length at the earlier stage. In this way, growth during each interval between stages is expressed in proportion to the amount of tissue or "meristematic capital" present at the beginning of the interval under study. In Figure 3, the same results are presented graphically.

These figures show that the amount of growth which takes place before the vascular pattern is laid down by procambial differentiation is only a small percentage of the total growth of the organ. Moreover, this percentage varies greatly from one species to another. The size of the primordium at the time of procambial differentiation is similar in all of the species studied, ranging from 186 micra in *Senecio vulgaris* to 294 micra in *Microseris nutans.* This range is far less than the extreme differences in size between mature achenes, so that the percentage of growth in length that takes place before procambial differentiation ranges from high figures to 14 to 16 percent in *Senecio cruentus* to the extremely low figure of 0.9 percent in *Tragopogon porrifolius.*

Two obvious conclusions can be made from these results. First, developmental patterns differ widely from one species to another of this family, and may even differ between varieties of the same species, as in *Helianthus annuus* and *Senecio cruentus.* Second, each of the tribes represented possesses a characteristic series of patterns that are different from those found in other tribes. In the Heliantheae, for instance, the greatest percentage increase in size occurs between procambial differentiation and xylem differentiation. The Cichorieae are more variable in this respect, but show a greater tendency than other tribes toward growth between anthesis and achene maturity.

A further conclusion can be drawn by comparisons between members of the same tribe. In both of the comparisons between cultivated varieties of the same species: wild vs. cultivated *Helianthus annuus* and the two cultivated varieties of *Senecio cruentus,* the greatest difference exists with respect to size increase between xylem differentiation and anthesis, a stage during which few or no mitotic divisions are taking place. In *Senecio,* this is also the stage at which the greatest difference exists between the two species studied: *S. vulgaris* and *S. cruentus.* In the Heliantheae, the two wild species of *Helianthus* differ most from *Wyethia glabra* with respect to the increase at this stage, but the greatest difference between *H. annuus* and *H. Bolanderi* is with respect to the stage between anthesis and seed maturity. In the Cichorieae, the most divergent species, *Tragopogon porrifolius,* differs most from the others with respect to this last stage.

These results support, in general, the hypothesis that later developmental stages are more easily modified at the level of varieties and species than are early stages. In all of the varietal and species comparisons, except for the species of *Microseris,* stages after xylem differentiation differ more than do earlier stages. Furthermore, the size of the primordium at the time of procambial differentiation is strikingly similar among all of the forms studied, at least in comparison to the much greater differences between their mature achenes. Finally, with respect to the two examples of artificial selection for increased size, genetic changes affecting later stages were established in preference to those affecting earlier stages.

The comparison between the two species of *Microseris* provides a significant exception to the above generalization. The annual species, *M. Douglasii,* differs from the perennial *M. nutans* with respect to the smaller size of the ovary primordium at the stage of procambial differentiation, and the proportionally greater amount of growth that takes place between this stage and that of xylem differentiation. This suggests that *M. Douglasii* arose from its perennial ancestor, which certainly was not *M. nutans*, but may have been a species having a similar developmental pattern, via reduction in the size of the ovary primordium, accompanied or followed by compensatory growth at later stages. This reduction, which affected an early developmental stage, may have been responsible for the reduction from ten ovarian bundles, which is characteristic of *M. nutans* and other perennial species of *Microseris,* to five bundles, as found in most or all of the annual species, including *M. Douglasii.*

This small and admittedly inadequate sample supports, as far as it goes, the hypothesis that large achenes having simple vascular patterns are derived by secondary enlargement from smaller ones having similar vascularization. With respect to the hypothesis that simplification of vascular pattern takes place via a "bottleneck" of reduction that affects early developmental stages, followed by secondary enlargement, the present evidence is inconclusive. I hope, however, to obtain an answer to this question when the study is complete.

A Basis For Differentiating Between Primary and Secondary Union of Parts

The second kind of situation that I would like to discuss concerns the validity of vascular patterns as evidence for the phylogenetic origin of "fusions" and "adnations" between parts. This topic has been much discussed in connection with the origin of the inferior ovary, or epigyny (Douglas, 1957; Kaplan, 1967). The extreme skepticism of Carlquist (1969) with respect to such evidence has been challenged by Kaplan (1971), who in my opinion has successfully answered many of Carlquist's criticisms. At any rate, since diverse vascular patterns are found in various genera having epigynous gynoecia, is association with other very different morphological characteristics as well as affinities to various groups having perigynous or hypogynous gynoecia, this evidence indicates strongly that the epigynous condition has been evolved many times independently in different orders of plants, by various evolutionary pathways.

In my discussion, however, I should like to focus attention on the androecium. The "fusion" of stamens into bundles or a tubular staminal column that includes the entire androecium is a familiar feature in several plant families, particularly the Malvaceae, Sterculiaceae, Hypericaceae (Guttiferae), Myrtaceae, and some genera of Dilleniaceae. This "fusion" is generally regarded as secondary (Eames, 1961), and in most instances this conclusion is well justified. Developmentally, it is most often brought about by a suppression of differentiation with respect to stamen filaments. Instead of separate intercalary meristems that produce the growth of each individual filament, a common meristem elevates some or all of the anther primordia on a single column, tube or sheath (van Heel, 1966).

Recent developmental studies, however, suggest that not all "fusions" between stamens are of this secondary kind. In *Paeonia* (Hiepko, 1965) and *Hypericum* (Leins, 1964; Robson, 1972) careful analyses of the development of floral primordia have shown that stamen bundles, not individual anther primordia, fit into the phyllotactic sequence that is followed by the other floral parts. Furthermore, anther primordia arise not from the undifferentiated meristem of the reproductive axis, but from distinct primordia of stamen bundles. Their differentiation precedes the activity of the intercalary filament meristem, which in

Paeonia and *Hypericum* elevates each stamen upon a separate filament.

The anatomical condition that follows this developmental pattern is that of a common "trunk" vascular strand for each cluster of stamens that are differentiated from the same bundle primordium. The vascular strands that supply individual stamens diverge from the "trunk" strand, not directly from the floral axis.

Examination of the vascular anatomy of the mature androecium in a number of relatively primitive angiosperms, such as *Degeneria* (Swamy, 1949), *Hibbertia* (Wilson, 1965), and certain Annonaceae (*Cananga, Goniothalmus,* unpublished observations of the present author), has revealed the same kind of bundle pattern in them. In most instances, this pattern is not accompanied by an obvious clustering of the stamens in the flower as viewed externally. This condition leads me to believe that, although in some instances such stamen bundles may have been derived from single stamens by a process of multiplication of another primordia, or "dédoublement," as Leins (1964, 1971) maintains, this has not always been so. Conclusions based upon comparisons between ovules and megasporophylls, which will be presented elsewhere, have led me to believe that among known fossil forms, those most nearly related to ancestors of the angiosperms are the cupule-bearing Pteridosperms such as Caytoniales (Thomas, 1925) and Corystospermaceae (Thomas, 1933). If this hypothesis is correct, then the structure of the microsprophylls in these forms should be considered. In no case do they consist of flat structures bearing sporangia upon their surfaces, as would be expected on the basis of the "classical" concept of the origin of stamens (Eames, 1961). They are always branched, and bear numerous microsporangia at the ends of the branches. The stamen bundles in genera like *Paeonia* could be derived from such microsporangiophylls by suppression of their branches.

This discussion can be summarized by stating the hypothesis that "fusions" of stamens are of two kinds. The existence of stamen bundles that are evident chiefly from examination of the vascular pattern, and are seen with difficulty or not at all when one examines the external structure of the flower, represents a primary fusion, which takes place at the very earliest stage of androecial development, and reflects an ancestral condition. On the other hand, the staminal tube of the Malvaceae, and the elevated clusters of stamens that are found in many genera of

Hypericaceae and Myrtaceae, as well as similar structures in various other families, are secondary in origin, and are produced by intercalary meristems that appear relatively late in development, after the anther primordia are fully differentiated. This hypothesis is entirely in accord with that of conservatism of gene complexes affecting early developmental stages.

A Plea For Further Research in the Field of Morphogenetic Taxonomy

The account which I have just given of the comparative development of achenes in the Compositae reports only the beginning of a small piece of research. Nevertheless, it shows that careful comparisons between developmental patterns of selected organs in a series of closely related forms can reveal similarities and differences that are not evident from examinations of mature organs. Moreover, some of these differences in pattern can serve as a guide to evolutionary direction.

In their efforts to broaden their field, botanists have, in recent years, been relying to an increasing extent on characteristics other than external morphology. Cytotaxonomy, based upon chromosomal differences, has been with us for a long time. More recently, chemotaxonomy has increased in popularity, and is yielding highly significant results. In my opinion, the essentially undeveloped field of morphogenetic taxonomy also needs to be developed. Its potential importance lies in the prospect that it may contribute more to our understanding of morphological taxonomy than any other field. The cytotaxonomist studies chromosomes as they appear during mitosis, when the DNA is condensed into neat packages, and the genes are inactive. Innumerable studies in this field have shown us that the number and shape of these "packages" is much less important for adaptation, survival, and ecological distribution than is the nature of the genes contained in them. Chemotaxonomists, because of the complexity of their field, have been forced to concentrate upon certain compounds and properties largely because of technical considerations that determine the ease of study rather than criteria of evolutionary significance. We have, therefore, many systematic comparisons of secondary and accessory compounds such as phenolics and terpenes, as well as of a single property, electrophoretic mobility, possessed by those proteins that are easily isolated and recognized. Important as these investigations are, they explore only the fringes of the biochemical systems of the organisms concerned.

The potential value of morphogenetic taxonomy arises from the fact that adult structures appear as a result of patterned sequences of gene action in development. Groups of genes are activated and deactivated according to a specific program that is controlled by a complex system of regulator genes (Britten and Davidson, 1969). Morphological evolution must be based ultimately upon mutations and recombinations of these particular genes. By developing the discipline of morphogenetic taxonomy, botanists may be able to approach closer to an understanding of how these genes work, and how they change during evolution.

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PROTOPTYCHUS, A HYSTRICOMORPHOUS RODENT FROM THE LATE EOCENE OF NORTH AMERICA

John H. Wahlert[1]

Abstract. The North American late Eocene *Protoptychus* Scott possesses an enlarged infraorbital foramen, a depression on the side of the snout anterior to this foramen for the origin of the anterior part of the middle masseter, tetralophate P^4–M^3, an enlarged incisive foramen, a deep pterygoid fossa, and apparently no stapedial foramen or carotid canal. These characters also occur in the Caviomorpha. With regard to the zygomasseteric structure and acquisition of an essentially molariform P^4, *Protoptychus* is more advanced than both its possible North American ancestor, which may be either a paramyid or *Mysops,* and *Platypittamys,* the most primitive Deseadan (Oligocene) caviomorph. The Protoptychidae, on present evidence, cannot be related closely to any rodents other than these. Pending further knowledge, the family is retained in the Protrogomorpha, but the possibility exists that it may be a specialized offshoot from the North American caviomorph ancestry.

Introduction

In the course of studying the cranial foramina of North American protrogomorphous and sciuromorphous rodents, I examined the type skull of *Protoptychus* (Princeton University 11235) and a second, much damaged facial region (PU 11230). I was immediately struck by features that set this form completely apart from all others I had at hand. These were the unusual shape and great posterior extent of the incisive foramen, the large size of the infraorbital foramen, the flatness of the sides

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of the snout, and the depression of an area on the snout anterior and extending somewhat dorsal to the infraorbital foramen. I was led, finally, to conclude that *Protoptychus* is a primitive hystricomorphous rodent possibly allied to the ancestry of the South American Caviomorpha. The lower jaw is present in specimens that I have not seen which belong to the Field Museum of Natural History; Turnbull (personal communication) is in the process of preparing these for description.

Taxonomic History of *Protoptychus*

The monotypic genus *Protoptychus* has had a checkered history in the literature of rodent taxonomy. Scott, in describing the skull of *Protoptychus hatcheri* from the Uinta deposits of Utah, stated: "That *Protoptychus* is an ancestral form of the *Dipodidae* seems abundantly clear." "It is not improbable that the *Heteromyidae* were derived from some form related to *Protoptychus,* though not from that genus itself" (1895: 280, 286). Matthew (1910: 68) followed Scott in associating the genus with the Dipodidae. Schlosser (1911: 427) created the subfamily Protoptychinae as one of two divisions of the family he termed Geomyoidea. Miller and Gidley (1918: 443) placed the subfamily back in the Dipodidae. Wood (1935: 239–240) stated that the tooth structure did not indicate close relationship to the Geomyoidea, and he noted that Schaub's studies on the jumping mice and dipodids eliminated them also as relatives of *Protoptychus.* He suggested that, instead, ". . . *Protoptychus* may represent an aberrant and sterile offshoot of the Ischyromyidae." Wood (1937: 261) formally raised the taxon to familial rank, Protoptychidae, as a division of the Ischyromyoidea. Simpson (1945: 78) and Wilson (1949: 99–100) followed Wood's familial designation and placement of the genus. A diagnosis of the family was published by Wood in 1955 (p. 171).

Dentition

Figure 1, a and b

In most respects Scott's description of *Protoptychus hatcheri* (1895) is accurate, but there are a few points that require reconsideration. He failed to notice the presence of a minute, peglike third premolar, and the revised dental formula (as noted

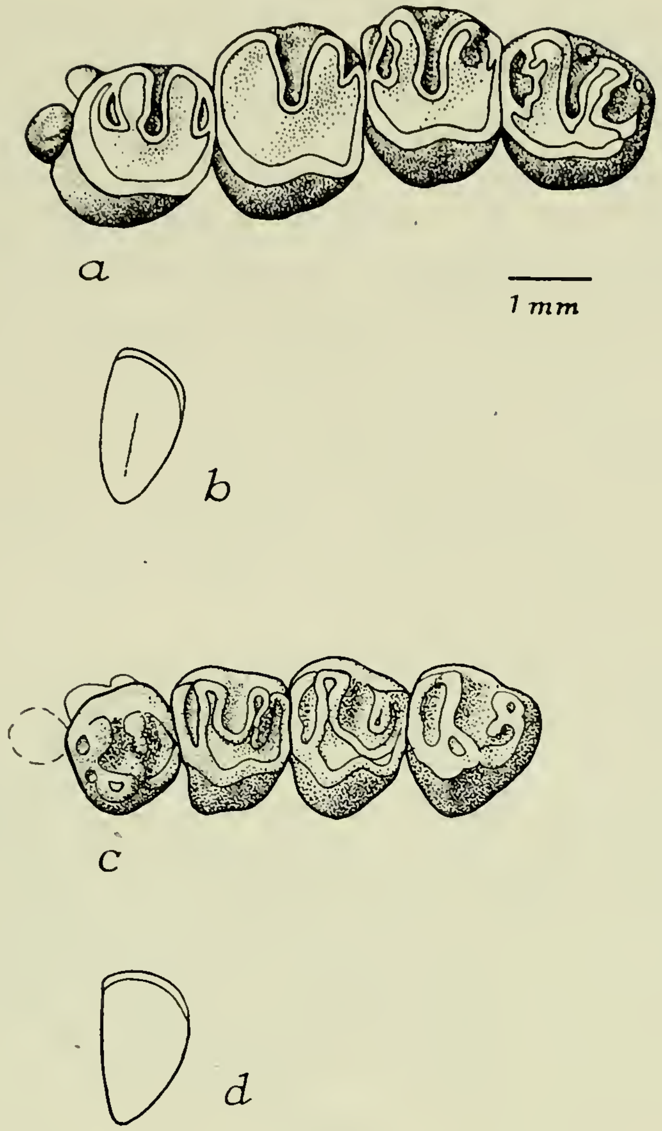


Figure 1. Dentition of *Protoptychus hatcheri* (PU 11235) : a. left cheek teeth, view perpendicular to wear surface; b. left incisor, cross section. Dentition of *Mysops parvus* (USNM 18043) : c. left cheek teeth, view perpendicular to wear surface; d. left incisor, cross section.

by Wilson, 1937: 450) is thus I^1 C^0 P^2 M^3. P^4–M^3 are brachyodont and notably higher crowned lingually than labially; although quite worn, they are clearly four-crested (Fig. 1a). The most conspicuous feature of the crown is a mesoflexus, which is broadest at the labial side and ends, at this stage of wear, near the middle of the tooth. The crowns of M$^{1-3}$ are grooved in the middle of the lingual side, the groove fading away well before reaching the base of the enamel; P^4 possesses only a vague suggestion of this groove.

Although the four molariform cheek teeth are lophate, the cusps are still readily compared with those in paramyid teeth as figured by Wood (1962: 8, fig. 1A). On the labial side the paracone and metacone flank the mesoflexus. The protocone is anterior to the lingual groove, and the hypocone, posterior; the crown is quadrate in outline. The paracone and protocone form the protoloph; the metacone and hypocone, the metaloph. The hypocone and protocone are already joined in the slightly worn M^3, and the metaloph is more broadly connected with the hypocone than with the protocone. A small, low mesostyle is present on the molars and is closely associated with the metacone in the first molar and with the paracone in the second and third molars; it increases in size posteriorly. No trace of it is to be seen in P^4. The four molariform cheek teeth possess both an anteroloph and a posteroloph. These are subordinate in importance to the two main crests on M^{1-2}, and are nearly equal to them in prominence in M^3.

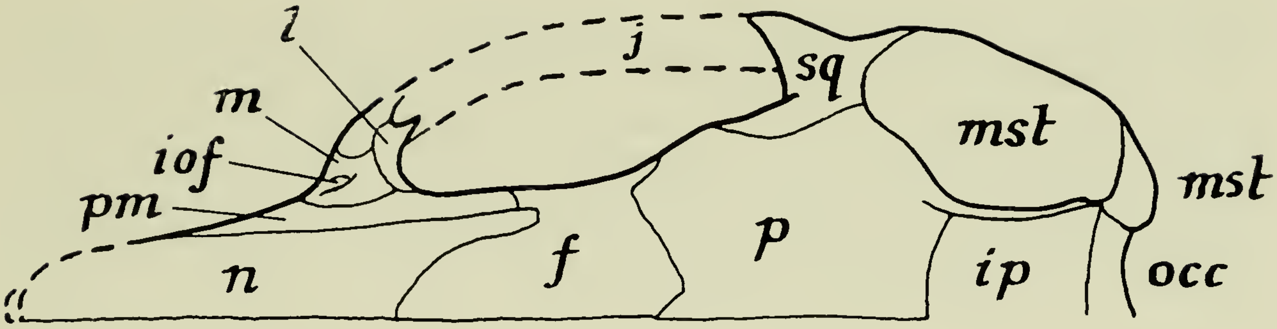
Scott remarked (1895: 270) that "the transverse crests visible on M^3 of *Protoptychus* (and doubtless in the unworn state of the other teeth, also) have a certain resemblance to the teeth of squirrels and spermophiles . . . ." In this he is correct because all retain in the upper dentition a relatively primitive arrangement of cusps. He continued, ". . . but the fundamental character of the tooth pattern is given by the enamel invaginations, which tend to divide it into two prisms. This arrangement is most like that found in *Pedetes,* the *Heteromyidae* and *Geomyidae.*" The mesoflexus, however, is not an invagination of the enamel from the lingual side of the tooth, it is simply a valley in the enamel between two worn crests; the crown is not divided into two prisms.

The incisor enamel as seen in a peel from the transverse break appears to be pauciserial. Pauciserial and multiserial enamels are similar, and a transverse section is not ideal for distinguishing them; the enamel is certainly not uniserial. Scott did not figure the incisor in cross section; the distribution of enamel

Figure 2. Skull of *Protoptychus hatcheri* (PU 11235); dorsal, lateral, and ventral views; sutures diagrammatic.

Key: stippled areas: bone missing, crushed, or matrix covered; dark area on snout: site of origin of masseter medialis; hatched areas: cross section of bone; dashed lines: structure reconstructed.

Bones: *ab* — auditory bulla, *as* — alisphenoid, *f* — frontal, *ip* — interparietal, *j* — jugal, *l* — lachrymal, *m* — maxilla, *mst* — mastoid, *n* — nasal, *occ* — occipital, *os* — orbitosphenoid, *p* — parietal, *pl* — palatine, *pm* — premaxilla, *sq* — squamosal. Foramina: *bf* — buccinator, *if* — interorbital, *iof* — infraorbital, *isf* — incisive, *jf* — jugular, *mf* — masticatory, *of* — optic, *paf* — post-alar fissure, *plf* — palatine, *sf* — stylomastoid.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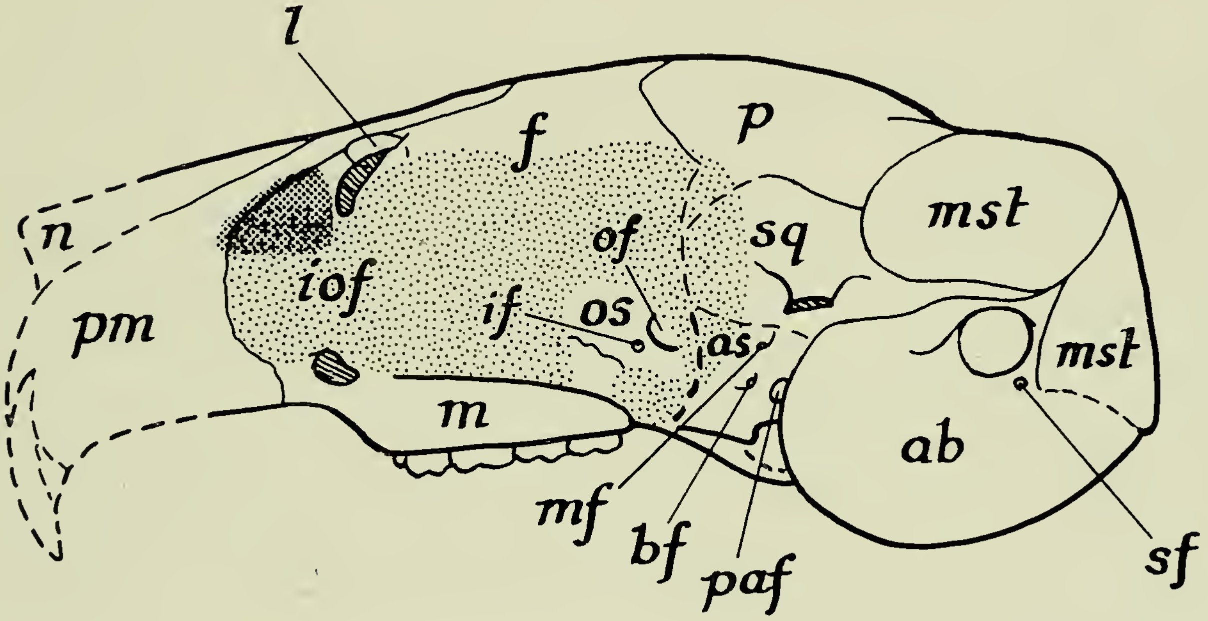
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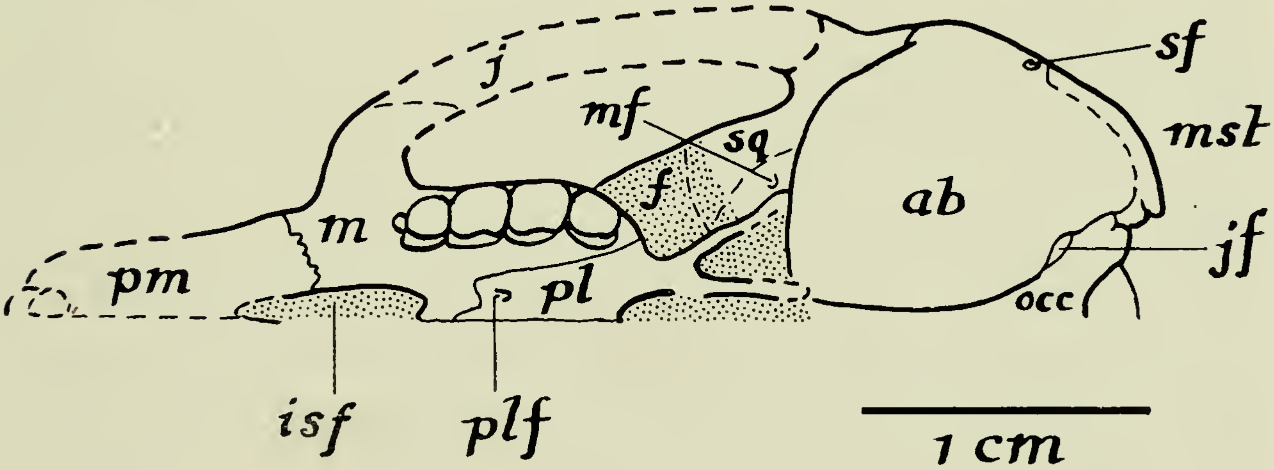
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on its front surface (Fig. 1b) is similar to that in many small Eocene rodents, *e.g.,* some species of *Paramys,* and of *Franimys, Sciuravus,* and *Mysops.* In transverse section the front of the incisor is less bowed than in these forms and has a marked posterolateral slant relative to the sagittal plane; it resembles the incisor of *Platypittamys* in this respect.

SKULL

Figure 2

Scott's description of the skull is adequate and accurate for the most part, but a few additional points can be made. The posterior extension of the nasal bones almost as far back as the middle of the orbits is, to my knowledge, unique to *Protoptychus* among rodents.

The auditory region is greatly inflated, and both the temporal and mastoid portions of the skull participate in this inflation. Scott stated that the ". . . mastoid bulla . . . is divided by partial septa into chambers, two of which are plainly shown, even externally, being bounded by deep grooves" (1895: 275). The two visible septae are seen only at the surface, and their extent is unknown. The region closely resembles that in *Chinchilla* except that there is no trace of a supraoccipital process that reaches the squamosal. In *Chinchilla* partial septae are present in the epitympanic sinus.

The parietal overlaps the dorsal epitympanic sinus laterally, and a narrow process of the parietal extends posteriorly beside the interparietal, apparently reaching the mastoid. Scott's dorsal view of the specimen (p. 270, fig. 2) shows the process arising from the parietal, although he incorrectly states in the text that the squamosal ". . . appears to send out a process between the parietal and the mastoid, which articulates with the interparietal" (1895: 276). The compression of the posterior part of the parietal and the unusual rectangularity of the interparietal seem to be in response to the great dorsal inflation of the epitympanic sinus. The back of the skull roof retains the primitive flatness and sharp angle with the occipital surface; it does not curve downward onto the occipital surface as it does in dipodids, heteromyids, and those caviomorphs in which the auditory region is also greatly inflated.

Many of the cranial foramina are preserved in the type specimen. The incisive foramina, unlike those of any protrogomorphous rodent, are unusually long, extending back to the middle of the fourth premolar, and their lateral margins are intersected anterior to the middle by the premaxillary-maxillary suture.

The infraorbital foramen is conspicuously larger dorsoventrally than that of any protrogomorphous rodent. The sides of the snout are flattened, and the course of the incisor root stands out as a swelling. Just anterior to the infraorbital foramen and extending somewhat dorsal to it is a depression on the side of the snout; this area appears to have been the site of origin of the anterior part of the medial masseter, which must have passed through the infraorbital foramen. *Protoptychus* was hystricomorphous.

In the orbital region, three foramina are visible. The optic foramen, of which only the ventral margin remains, is clearly a large aperture in comparison with those of paramyids, and is probably the structure which Scott (1895: 278) called "a large sphenoid fissure." Anteroventral to the optic foramen in the orbitosphenoid is a small aperture, possibly an interorbtial foramen. A foramen occurs in this position in various unrelated rodents, *e.g., Ischyromys, Geomys,* and questionably in *Castor,* and I attach no special taxonomic significance to its presence here. In the floor of the orbit is a dorsal palatine foramen, which transmitted the descending palatine artery. In *Paramys* this foramen shares a common opening with the sphenopalatine, whereas in *Protoptychus,* as in *Sciuravus,* the foramen is in the orbital floor posterolateral to the sphenopalatine foramen. The posterior palatine foramen, the exit for the artery, is wholly within the palatine, the primitive condition for rodents.

The margin of the sphenoidal fissure and most of the region where the alisphenoid, parietal, frontal, and orbitosphenoid come close together is crushed. The masticatory and buccinator foramina open upward and forward, respectively, near the back of the alisphenoid bone. Retention of separate foramina for the masseteric and buccinator nerves is a primitive rodent character. Posterior to the buccinator foramen there is an emargination of the alisphenoid, which, with the anterior side of the bulla, makes a foramen. A multiple aperture in the position is present in *Reithroparamys;* there is no comparable foramen in other paramyid skulls or in *Sciuravus.*

The postglenoid and the temporal foramen are absent, probably because of the greatly inflated bullae. The stapedial foramen, carotid canal, and mastoid foramen appear to be absent, but they (especially the last two) may have been obliterated by the slight lateral crushing which the specimen has suffered. The pterygoid fossa is very deep, and inadequately preserved for full description.

Discussion

By the process of elimination it is possible to rule out relationship to any rodent group except the Paramyidae, the genus *Mysops,* and the Caviomorpha. Of the protrogomorphous rodents, all but the Paramyidae and *Mysops* are significantly different from *Protoptychus.*

In 1959 Wood (p. 359) thought that the Protoptychidae might have been derived from the Sciuravidae; sciuravids are primitive in most skull characters and in this respect could be ancestral. However, the cheek teeth and their incipient crests are not nearly so primitive. Unlike the condition in *Protoptychus* and paramyids, the medial valley of the crown is open lingually and blocked labially by the mesostyle. Wilson (1949: 91) noted this and other characteristics of the cheek teeth as being markedly different from those of most paramyids.

The cheek teeth of *Protoptychus* are advanced over those of paramyids in that the third premolar is greatly reduced, the fourth premolar and third molar are tetralophate, and the metaloph is more closely connected with the hypocone than with the protocone. The major cusps, however, are still readily identifiable, and the anteroloph and posteroloph are not quite equal in prominence to the crests formed by these cusps. The basic pattern is most nearly comparable to that of *Paramys* and *Reithroparamys.* Some reduction of the third premolar has already occurred in *Reithroparamys.* Wood (1962: 248) tentatively suggested derivation of *Protoptychus* from *Reithroparamys* but stated, "On the other hand there are some undescribed specimens (including skeletons) that seem to suggest other relationships for *Protoptychus*." These remain undescribed.

The cheek teeth of the Ischyromyidae (including only *Ischyromys* and *Titanotheriomys*) are very similar. However, the infraorbital foramen is much smaller, and the zygomatic plate is tilted, indicating a trend toward a sciuromorphous type of masticatory musculature[1]. The dorsal palatine foramen is well inside the sphenopalatine foramen; the pterygoid fossa, though well developed, is not nearly so deep; and there is a well-defined carotid canal in ischyromyids.

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[1] Having examined the evidence, I agree with Wood (1937: 195) rather than Black (1968: 275) on this point.

The cylindrodontids[1], specifically *Ardynomys,* which has four-crested cheek teeth, differ in detail. The dorsal palatine foramen is not separated from the sphenopalatine; the pterygoid fossa is shallow, and the carotid canal is present although small.

The Eocene rodent that most closely resembles *Protoptychus* is *Mysops.* There are three differences between the molariform teeth of the two genera (cf. Fig. 1c and d). In *Mysops* the anteroloph of P^4 is not fully developed as a continuous crest; the metaloph is incomplete and does not meet the hypocone, though its trend is toward the anterior part of that cusp; and whereas in *Protoptychus* the cusp is prominent, in *Mysops* it is a very minor one. As seen in transverse section, the incisors of *Mysops* are very similar to those of *Protoptychus,* but the anterior surface is more bowed. The alveolus for P^3 indicates that in *Mysops* the tooth was not reduced. A striking bit of evidence for relationship between the two genera is that in *Mysops* the length ratio of the incisive foramina to diastemal length exceeds .60, a ratio greater than that known for any protrogomorphous rodent (Wahlert, 1972). Although the foramina do not extend as far back as the first premolar, as in *Protoptychus,* their size suggests a stage intermediate between a paramyid or sciuravid and *Protoptychus.*

The Aplodontoidea, even the earliest ones, are so different in cusp pattern that close relationship to them can be ruled out. Prosciurids, which are most likely ancestral to aplodontoids, differ in the same regard. In them the pterygoid fossa is not deep, and there is a conspicuous stapedial foramen.

There is nothing about the dentition of *Protoptychus* that suggests relationship to the Hystricidae, which, to judge from their geologic record, may have been of Oriental origin (Wood and Patterson, 1970: 636).

The phiomyids, most notably *Metaphiomys,* bear some similarity to *Protoptychus* in that they are hystricomorphous and also have enlarged incisive foramina (Wood, 1968). The cheek teeth, however, are quite different; the crown pattern of *Protoptychus* is four-crested, whereas those of *Phiomys* and *Metaphiomys* are five-crested, the fifth crest being the mesoloph. Likewise the cheek teeth of the theridomyids differ in having five crests.

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[1] Wilson (*e.g.,* 1949: 93) and Wood (personal communication), on the basis of dental similarity, place *Mysops* in the Cylindrodontidae. I hesitate to accept this assignment because, in the one partial skull of the genus (USNM 18043), the incisive foramina are considerably longer relative to the diastemal length than in *Cylindrodon, Pseudocylindrodon,* and *Ardynomys.*

Myomorphous rodents can be excluded from possible relationship because the cheek tooth cusp pattern is essentially different. All sciuromorphous forms can be eliminated because of their zygomasseteric structure. Furthermore, the stapedial artery, which may well have been lacking in *Protoptychus,* is retained and its foramen is conspicuous in heteromyids and eomyids; in sciurids the foramen is present although less easily seen.

The remaining group for consideration is the Caviomorpha. The Caviomorpha are hystricomorphous; many of the early South American members of the group, *e.g.,* the Deseadan *Cephalomys* (Wood and Patterson, 1959: 343, fig. 21), *Sallamys* and *Incamys* (Patterson and Wood, in preparation), and several Santacruzian genera illustrated in Scott (1905) have elongate incisive foramina. The living caviomorphs lack the tympanic portions of both the stapedial and internal carotid arteries (Guthrie, 1963: 478; Bugge, 1971: 532), as is quite possibly the case in *Protoptychus.* The pterygoid fossa is very deep in caviomorphs.

The cheek teeth of *Protoptychus* are lophate and are based on a series of four crests that are fully homologous with those of primitive caviomorphs. *Protoptychus* retains a small but distinct mesostyle on the molars which is lacking in caviomorphs, except *Branisamys luribayensis,* which has the cuspule on the second molar (Hoffstetter and Lavocat, 1970: 172 and fig.); it lacks the lingual valley, the hypoflexus, which is prominent in caviomorphs, but does have an indentation in that position. The fourth premolar of *Protoptychus* is molariform, unlike those of the more primitive Deseadan caviomorphs, *Deseadomys,* and *Platypittamys,* but shows some resemblance to one specimen of *Sallamys* (Patterson and Wood, in preparation).

The incisors, as noted above, appear to have pauciserial enamel. This is a plausible condition for a caviomorph relative, since multiserial enamel was surely derived from pauciserial (Korvenkontio, 1934; Wahlert, 1968: 13), and the two are not very different, bands of the inner enamel layer in each being several prisms wide.

The simplest taxonomic interpretation of *Protoptychus* is to call it a hystricomorphous member of the Protrogomorpha. Structural details which are like those found in caviomorphs would be attributed either to convergence or to parallelism stemming from common ancestry within the Protrogomorpha. The consequence of this interpretation would be that the hystricomorphous condition of the masseter and infraorbital foramen arose more than once from the protrogomorphous condition, a conclusion in keeping with the similar multiple origin of sciuromorphous musculature, *e.g.,* independently in *Titanotheriomys,* and with its presence as a component of the myomorphous condition. *Mysops* may be a close relative of *Protoptychus,* but until a good skull of the genus is known this can be taken as no more than a possibility. The specialized characteristics of *Protoptychus,* especially those associated with the masseter and with the auditory region, confirm the need for a separate family to receive the genus.

Protoptychus could be a caviomorph, but, on the basis of the earliest forms known, a rather complicated explanation would be required. There are three anatomical barriers to placing *Protoptychus* in the Caviomorpha: its precociously molariform (*i.e.,* four-crested) fourth premolar, the lack of a distinct hypoflexus in the molars, and its hystricomorphous condition. According to Wood (1949) the most primitive Deseadan caviomorph[1], *Platypittamys,* has only a slightly enlarged infraorbital foramen, which did not transmit any part of the masseter, and a simpler fourth premolar than any paramyid known at the time of its description; whether the condition of the premolar was primitive or reduced could not be determined. On the basis of an undescribed Gray Bull paramyid, Wood and Patterson (1959: 296–297) were able to ascertain that the absence of a separate metaloph in the fourth premolar of *Platypittamys* and some other Deseadan caviomorphs is primitive. The Gray Bull paramyid, *Franimys,* was described by Wood in 1962 (pp. 139–147). The fourth premolar is comparable and also simple.

Although the cheek tooth patterns of *Protoptychus* are closer to those of *Paramys, Reithroparamys,* and *Mysops,* it is possible to derive them from that of *Franimys.* The direct ancestor of the South American Caviomorpha would then have been primitive in comparison with its closely related North American contemporaries. Wood and Patterson (1959: 406) stated, "The South American rodents were not descended from immigrants from Wyoming, but rather from rodents that lived in some part of middle America or southeastern United States, regions from which the Eocene mammalian faunas are essentially unknown." The rarity of *Protoptychus* in fossil collections supports the possibility that it, too, is based in a stock evolving elsewhere than in the western United States.

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[1] The caviomorphs described by Hoffstetter and Lavocat (1970) from the Deseadan of Bolivia are more advanced in that they already have enlarged infraorbital foramina and the posteroloph in some is divided into two parts (I do not agree that a mesoloph is present).

Until the lower jaw of *Protoptychus* is described, however, retention of the hystricomorphous Protoptychidae in the Protrogomorpha seems advisable for the present, since a hystricomorphous skull can accompany a sciurognathus jaw (*e.g.*, *Pedetes*). The similarities to caviomorphs are very suggestive nevertheless. The future may reveal that *Protoptychus* was a precociously specialized offshoot of the northern group from which caviomorphs arose.

ACKNOWLEDGMENTS

I am indebted to Albert E. Wood and Bryan Patterson for their guidance; to the vertebrate paleontology staff at Princeton University for permitting me to study the specimens; and to Barbara Lawrence and Charles Mack of the Mammal Department, Museum of Comparative Zoology, for making modern comparative material available to me. I would also like to thank both Carol C. Jones for unbiased corroboration of my views of structural details, and Katherine H. Wahlert for aid with the manuscript.

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Addendum

Since this manuscript was submitted, W. D. Turnbull (personal communication) has provided me with a description of the lower jaw in a Field Museum specimen of *Protoptychus;* only the outside of the jaw has been prepared so far. Turnbull states, "The masseteric fossa of the lower jaw is distinct but shallow, and the angle is laterally offset and rather attenuated. From the offset angle and the appearance of the junction of the angle with the ramus, I'd say it had a well developed pars reflexa to the masseter, but I've not seen the medial side so know nothing about its area of insertion." He concludes that the jaw was probably quite hystricognathus. This evidence adds support to the hypothesis that *Protoptychus* is related to the caviomorph rodents through common ancestry either within the paramyids or within a Middle American caviomorph population that is as yet unknown.

B R E V I O R A

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ENVIRONMENTAL FACTORS CONTROLLING THE DISTRIBUTION OF RECENT BENTHONIC FORAMINIFERA

Gary O. G. Greiner*

Editorial Introduction

Gary Greiner lost an eight-year battle with cancer and died in January 1973 at the age of 31. His unconventional approach to paleontology belied the painfully shy and unassuming character that many might have taken, so wrongly, as marks of merely ordinary ability. He was an original and radical thinker, limited, frustrated, even exasperated, by the reception that must attend unconventional ideas (be they right or wrong). And it was his special tragedy that illness, with its ultimate and ineluctable result, struck even before he began his research and robbed him of energy and time to test the ideas that flowed so readily.

Gary was captivated by D'Arcy Thompson's approach to form — to the reduction of organic complexity to a few, simple generating factors related to physical forces in the environment. D'Arcy Thompson overstated his case for the complex Metazoa, but it represents an insight scarcely explored (though surely more appropriate) for simpler Foraminifera. Gary asserted this theme within a traditional area of natural history fundamentally hostile to it (foraminiferal systematics) — an area that catalogues the specific, the unusual and the peculiar in preference to extracting the simpler regularities that have both general significance and frequent exceptions.

This paper represents Gary's views on the control of relative abundances by a simple environmental factor. Specialists will recognize some exceptions among forams in other parts of the

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world. They may disagree with his unsupported speculations on the significance and mode of formation for different types of calcareous walls. Yet the data on distribution are firm and must be explained. We hope that readers will focus on the power of Gary's unconventional approach, on his search for reduction and cause in preference to elaboration and minute, thoughtless description.

As an appendix, we attach the short text of a talk delivered to the annual meeting of the Geological Society of America in 1970. It supplements, in a broader evolutionary context, the central notion of physical control so central to the functional theme of causal correlation between environment and form. We report with the greatest regret that we were unable to reconstruct Gary's major work from his fragmentary notes and copious data — a bold attempt to synonymize virtually all the agglutinating Foraminifera of the Gulf of Mexico by showing that the entire range of form (now attributed to several genera) can be generated automatically by the interaction of a varying environment and the few parameters (sensu Raup and Vermeij) needed to specify construction of the seemingly complex foraminiferal test.

Gary wrote the following paper during a post-doctoral year at the Museum of Comparative Zoology. It was our privilege to have known, better than most others, such a courageous and talented person.

Stephen Jay Gould
Alan D. Hecht

ABSTRACT. The relative abundance distributions of the three major groups of benthonic Foraminifera (agglutinated, porcelaneous, and hyaline calcareous) from the northern Gulf of Mexico paralic environments have been studied to determine the environmental factor, or factors, actually controlling the distribution. The relative contribution of each type to the total foraminiferal fauna is related to temperature and/or salinity within each bay studied, and to regional gradients in temperature and salinity (expressions of climatic and physiographic interactions) throughout the northern Gulf estuaries.

I conclude that these correlations can be explained on the basis of foraminiferal interaction with a single environmental factor — availability of calcium carbonate for use in construction of tests. This factor depends, to a large extent, on salinity and temperature in shallow, marine or brackish waters.

Agglutinated Foraminifera do not require calcite to build their test; they dominate the faunas in areas of low $CaCO_3$ availability. Porcelaneous Foraminifera employ no nucleating surface for calcite crystal growth; crystals develop in a random array within a cytoplasmic layer. They dominate in areas of high $CaCO_3$ availability, but diminish in abundance toward lower values owing to difficulties in secretion of calcite. Hyaline calcareous Foraminifera produce oriented calcite crystals grown on an organic nucleating surface. This surface permits secretion of calcite for test construction in areas of lower $CaCO_3$ availability than is possible for the porcelaneous types, but the need for an ordered structure prevents their thriving in areas of hyper-supersaturation. Calcareous Foraminifera can dominate agglutinated types when $CaCO_3$ is readily available, through occupation of niches unavailable to the latter (*e.g.*, on marine plants). Thus, hyaline calcareous Foraminifera dominate in areas of intermediate $CaCO_3$ availability.

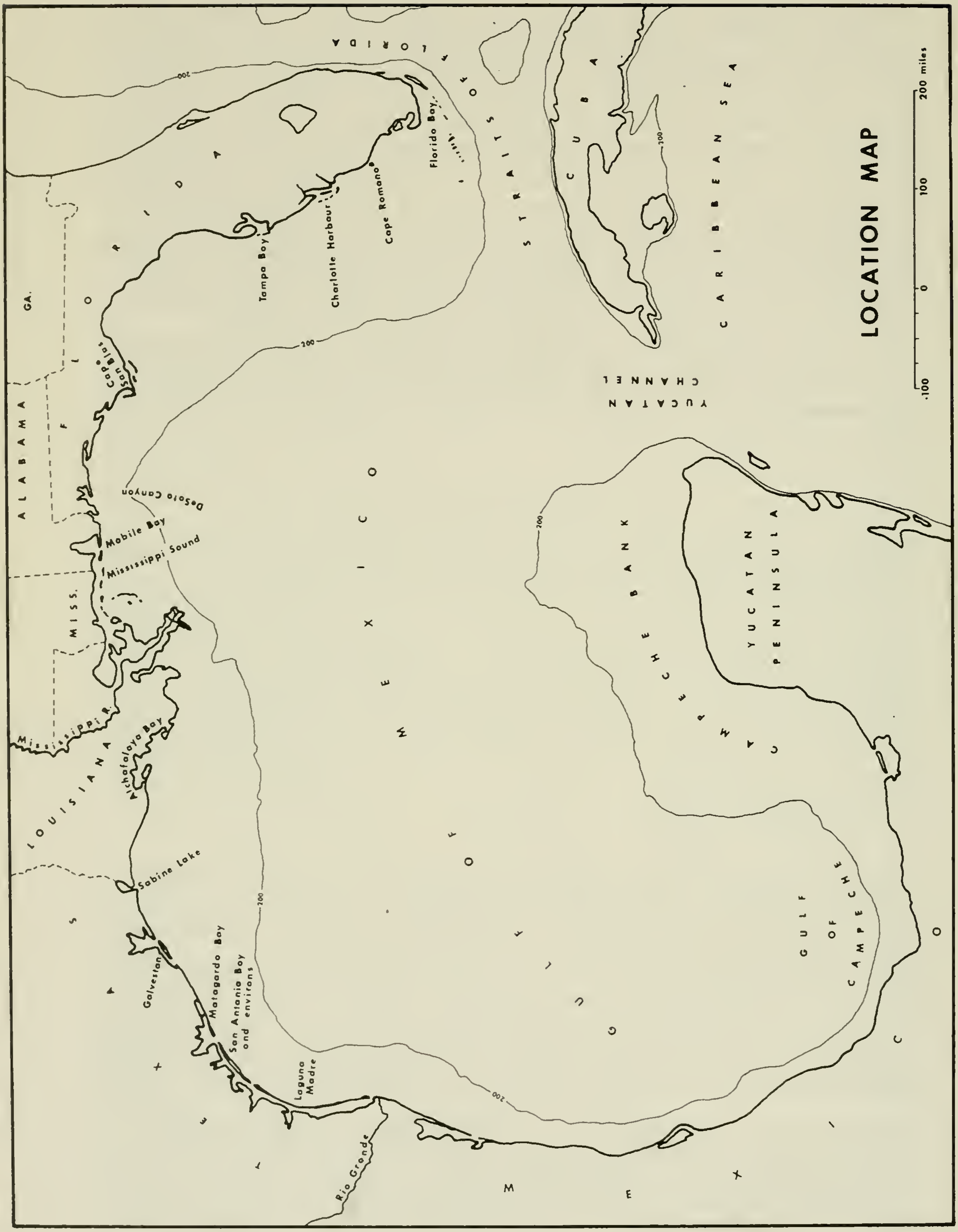
If we accept this simplistic approach to the study of Foraminifera, then its ramifications might have far-reaching effects in the study of foraminiferal paleoecology, since the applications would be independent of specific or generic classification.

INTRODUCTION

Most ecologic studies of Recent Foraminifera have dealt with distributions of the various *species* or *genera* present in a particular area, and with the correlation of these distributions with various environmental parameters. The reasons for these correlations are difficult to ascertain; hence, the applicability to the fossil record of conclusions based on such correlations is often doubtful. To extend ecological inferences of a particular faunal group to paleontologic situations, an understanding of environmental interactions with morphologic characteristics transcending specific or generic classifications should be sought.

I chose foraminiferal wall type as the character to investigate (Greiner, 1969). In standard classifications (Loeblich and Tappan, 1964), wall type is used to separate the three major groups of Foraminifera into suborders — the Textulariina (agglutinated walls), the Miliolina (porcelaneous, calcitic walls), and the Rotaliina (perforate, hyaline calcareous walls). If the influence exerted by the environment on the distribution of these separate suborders could be recognized, the information gained could reasonably be extrapolated to paleoecologic interpretations of faunas as early as the beginning of the Mesozoic Era when calcareous Foraminifera were becoming abundant.

In the Recent, the relative contributions of each of these groups to the total fauna vary systematically across the continental shelf, from one bay to another, and from boreal waters to the tropics. That these changes are systematic and simple, rather than sporadic and complex, suggests that the abundances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Florida Bay
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Charlotte Harbour
Tampa Bay
Cape San Blas
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L O U I S I A N A
T E X A S
Mississippi R.
Atchafalaya Bay
Sabine Lake
Galveston
Matagordo Bay
San Antonio Bay and environs
Laguna Madre
Rio Grande
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Y U C A T A N C H A N N E L
C A R I B B E A N S E A
C U B A
S T R A I T S O F F L O R I D A
DeSoto Canyon
Mobile Bay
Mississippi Sound
200

Figure 1. Location map.

of the foraminiferal suborders are being controlled by some general property of the environment, and that this property also varies simply and systematically. I assumed that a careful analysis of these distributions in relation to general environmental parameters would result in *correlations* leading to an understanding of the actual *controlling* factor or factors. Depth, the one factor suggested by Phleger (1960a) as most significant in controlling distributions of foraminiferal species in offshore traverses, can be essentially eliminated from consideration by investigation of faunas in very shallow water bodies — bays, lagoons, and sounds. Variation in the faunas can then be ascribed to some other environmental factor, such as temperature, salinity, character of the substrate, or some critical combination of several of these.

Foraminiferal faunas and general environmental parameters have been described for many of the larger bays, lagoons, and sounds adjacent to the northern Gulf of Mexico (Fig. 1). Since we have adequate literature on these shallow water bodies and since they form a geographic, as well as an environmental, continuum, they have been chosen for more complete analysis.

The purposes of this study are, then, to describe the relative abundance distributions of the three major groups of benthonic Foraminifera in the estuarine environments of the northern Gulf of Mexico; to relate these distributions to physical and chemical parameters of the environment; to review the more recent literature pertinent to the understanding of physiologic mechanisms employed by the foraminifers in constructing each wall type; and, finally, to summarize the environmental factors and relate them to the physiologic processes of wall construction by these protists, with a view to determining the actual *causes* of distribution at this morphologic level.

The results, it is hoped, will have a general significance for the interpretation of the paleoenvironments and paleoclimates of geologic epochs prior to those populated by species that still exist today.

Previous Studies of Foraminiferal Ecology

The early works on Recent foraminiferal ecology (*e.g.,* Parker, 1948; Phleger and Parker, 1951; Parker, Phleger, and Peirson, 1953; and Bandy, 1956) were largely taxonomic, with descriptions of species distribution in relation to depth and geographic position, based on relative abundances at each sample locality.

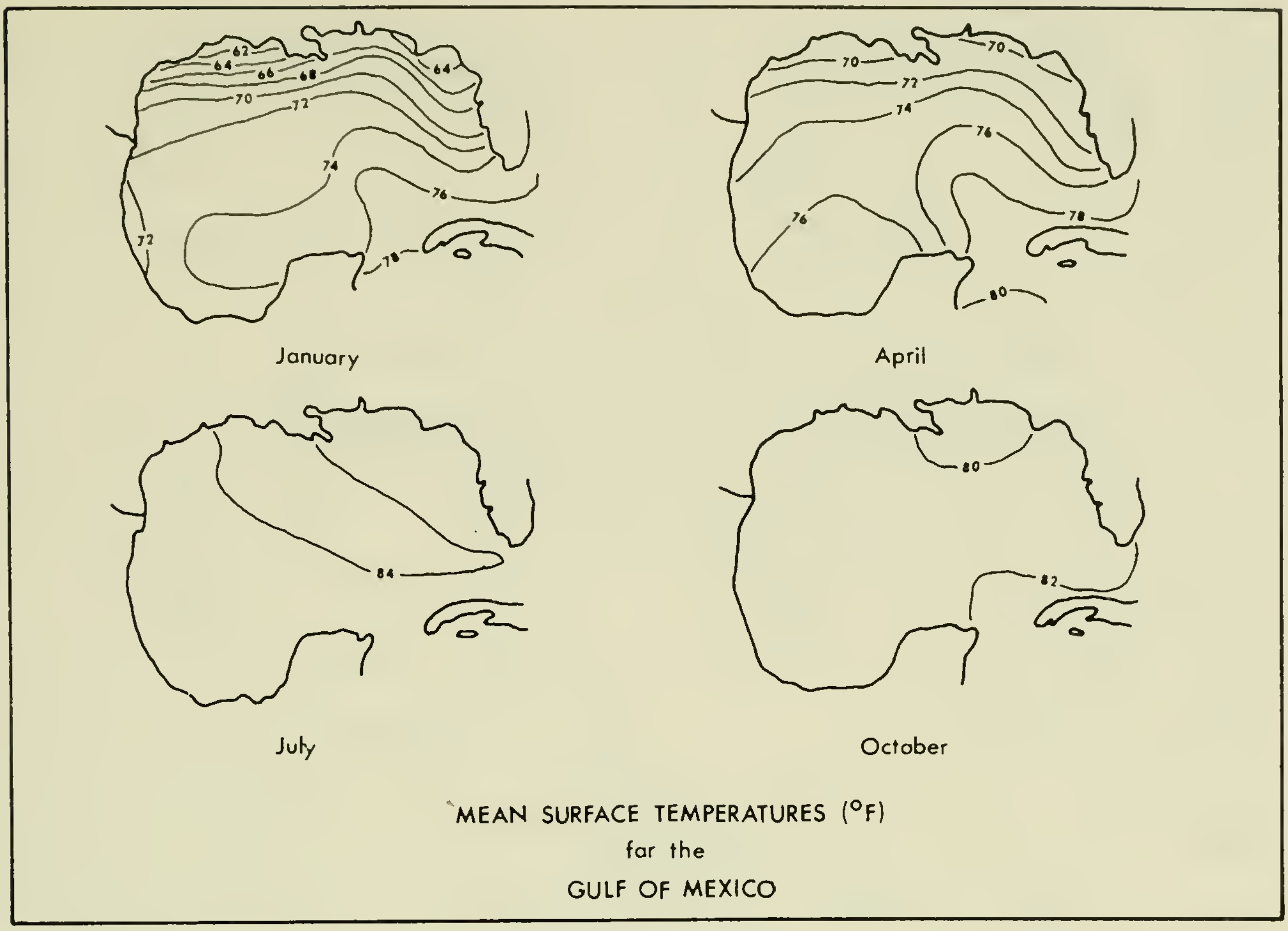
Various environmental parameters were invoked to explain the apparent natural breaks in faunal patterns. Since depth and proximity to the shore and continental shelf break had been measured, and since little else was known about the environment of the open ocean, discontinuities in the distributions were correlated with these factors.

Later studies show similar approaches to the problem of causes for the observed distribution patterns. A notable example is that of Lidz (1965), who observed intercorrelations of various environmental factors and species distributions measured in Nantucket Bay, Massachusetts. The most that could be said, based on the correlations, is that all of the factors are interrelated and correlated with one another, *i.e.,* the environmental factors are, to varying degrees, dependent variables. But nothing can be said about actual *causes* of the foraminiferal distributions.

Phleger (1960a), in discussing the ecology and distribution of Recent Foraminifera, states that the *causes* of depth zonation and other distribution patterns are not clearly known. The factors involved (he states) are temperature, salinity, food, water chemistry, pressure, currents, turbidity, turbulence, substrate, biologic competition, disease, etc. And in summarizing this long list, he states that at the present state of our knowledge it is not possible to evaluate any one of these factors. In a later report of the state of the field (Phleger, 1964), he indicates that ". . . there is little or no specific information on the interactions between the patterns of benthonic foraminiferal faunas and the natural environments which control these patterns."

A few, more current papers reflect this state of affairs and illustrate attempts to define characteristics of foraminiferal populations (diversity, planktonic/benthonic ratios, general morphology, etc.) which transcend specific or generic characteristics and which are explicable in terms of the environment (Bandy and Arnal, 1960; Bandy, 1964; Phleger, 1964; Stehli, 1966; Wantland, 1967).

Funnell (1967) summarizes our knowledge of foraminiferal ecology in a discussion of Foraminifera as depth indicators in the marine environment. He suggests that since Foraminifera are studied with relation to depth, and depth has so many factors correlated to it, we can construct good interpretations for the Tertiary of, say, the Gulf Coast as compared to the Recent Gulf of Mexico, but that these same conclusions will not be necessarily valid for the Tertiary of, for example, northwestern Europe, or for the pre-Tertiary of the Gulf Coast.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MEAN SURFACE TEMPERATURES (°F)
for the
GULF OF MEXICO

Figure 2. Mean surface water temperatures during four months of the year for the Gulf of Mexico. (Redrawn from charts supplied by the National Oceanographic Data Center, 1966.)

Clearly then, the *causes* of various trends in foraminiferal faunas must be established, if situations in the fossil record fundamentally dissimilar to the time or area of Recent investigations are to be treated profitably.

Physico-Chemical Setting of the Gulf of Mexico

The coastal United States bordering the northern Gulf of Mexico is generally a broad, low-lying plain. The near-shore, shallow-water environments are made more complex by the presence of many barrier islands closely paralleling the coastline and often restricting the free interchange of river and open Gulf waters. The presence of the barrier islands produces many bays, lagoons, and sounds (Fig. 1), which harbor faunas distinct from those of the open Gulf. The temperatures and salinities of the water in these estuarine environments are a result of the interaction of various climatic and physiographic parameters of the region.

There is a definite increase in mean annual temperature (re-

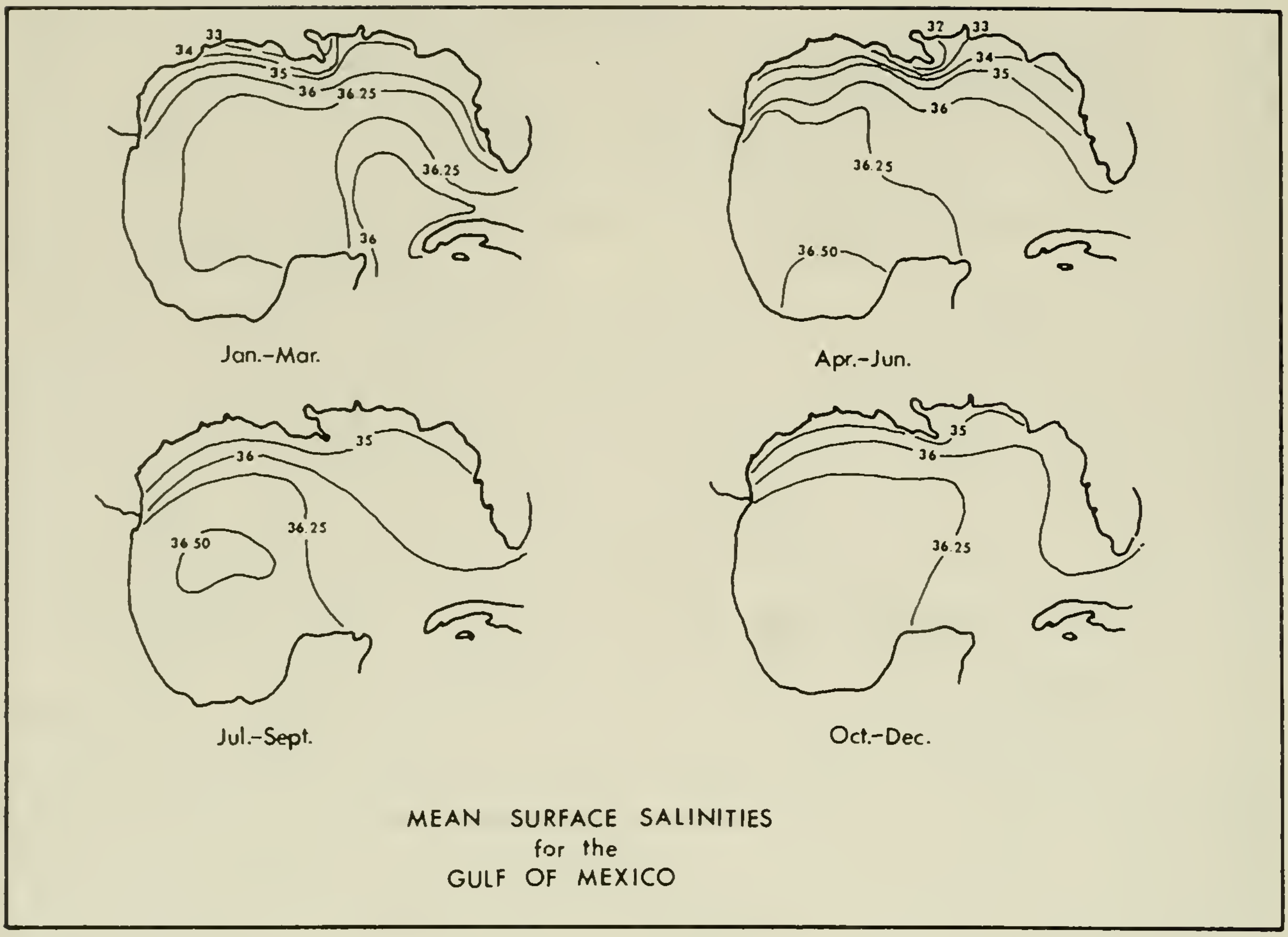

Figure 3. Mean surface water salinity during four seasons of the year for the Gulf of Mexico. (Redrawn from charts supplied by the National Oceanographic Data Center, 1966.)

flected in the Gulf surface water temperatures, Fig. 2; and in the January normal isotherms of Fig. 9) from north to south across the region. Since the bays are generally quite shallow, and hence the water well-mixed by wind, temperatures in them tend to correspond to air temperatures. Thus, mean annual water temperatures in the estuarine environments around the northern Gulf are lowest in Mobile Bay-Mississippi Sound and Sabine Lake, and increase in the more southern bays, being highest in Florida Bay and Laguna Madre.

Salinity values in the bays similarly show an increase from north to south. This is the result of several interrelated factors — precipitation, runoff, evaporation, and salinity of adjacent Gulf water (Fig. 3). The first three factors have been studied by Thornthwaite (1948) and the net effect plotted on a map as moisture budget isopleths (reproduced here as part of Fig. 9), which are an indication of moisture surplus (positive values) and moisture deficit (negative values). In general, low salinity values in the bays are associated with high moisture surpluses, as fresh-water influx into an enclosed shallow water body prevents, to varying degrees, the encroachment of higher salinity Gulf water (*e.g.,* Mobile Bay-Mississippi Sound and Sabine Lake). (See discussion by Phleger, 1954: 604). On the other hand, high salinity values are associated with moisture deficiencies. In this case the evaporation of lagoonal water permits entrance of higher salinity Gulf water and subsequent concentration of dissolved salts (*e.g.,* Laguna Madre). The general increase in salinity of open Gulf water from north to south (Fig. 3) enhances this estuarine environmental continuum of increasing salinity, observed from Mobile Bay-Mississippi Sound to Laguna Madre on the west and to Florida Bay on the east.

Through the interaction of these climatic and physiographic factors, then, an environmental continuum of increasing temperatures and increasing salinities is produced in the shallow water bodies under consideration here, from Mobile Bay-Mississippi Sound and Sabine Lake with lowest values, through Matagorda Bay and San Antonio Bay and environs on the west and Tampa Bay and Charlotte Harbour on the east with intermediate values, to Laguna Madre and Florida Bay with highest values.

Discussion of Foraminiferal Distributions

From published tables of species abundances in various estuarine environments around the northern Gulf of Mexico, I calculated the relative abundance of individuals possessing each of the three major wall types at given sample locations. This is based on percentage of individuals in the total (living plus dead) foraminiferal fauna. I then plotted these percentages on maps of the sample distributions and contoured the values.

The relative abundance distribution of the three foraminiferal groups will be discussed in detail for three of the estuarine environments — Mobile Bay-Mississippi Sound, Tampa Bay, and Laguna Madre — and more broadly for the others, to demonstrate correlations with temperature and salinity on the local scale. Following this, I will consider the faunal dominance by each of the groups through all the bays, lagoons, and sounds adjacent to the northern Gulf to document similar correlations with these environmental factors on a regional scale.

MOBILE BAY-MISSISSIPPI SOUND

The distribution of Foraminifera and possible ecologic factors affecting the distribution in Mobile Bay, Alabama, have been briefly mentioned by Walton (1964). Phleger (1954) has made

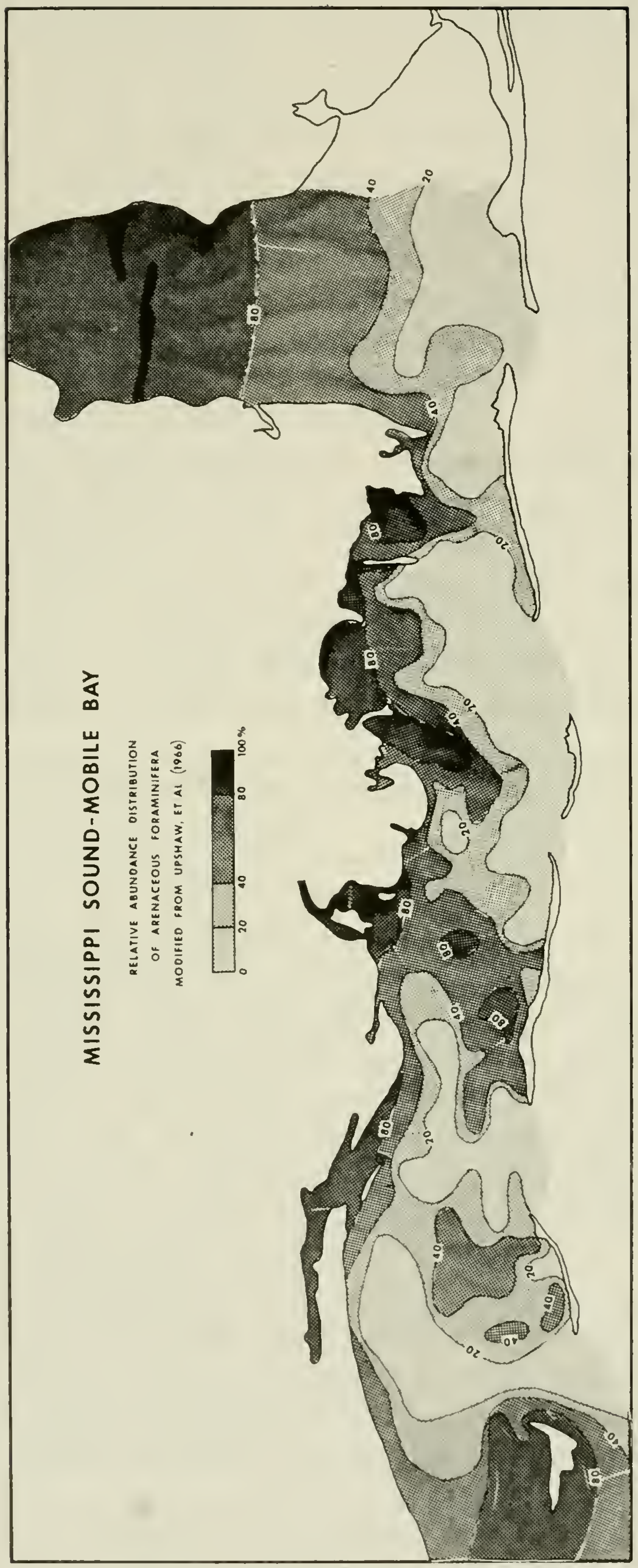
MISSISSIPPI SOUND-MOBILE BAY
RELATIVE ABUNDANCE DISTRIBUTION
OF ARENACEOUS FORAMINIFERA
MODIFIED FROM UPSHAW, ET AL (1966)
0
20
40
80
100%
20
40
80

Figure 4. Relative abundance distribution of agglutinated Foraminifera from Mobile Bay-Mississippi Sound. (After Upshaw *et al.*, 1966.)

a similar but more detailed study of the Mississippi Sound. Upshaw *et al.* (1966) have studied and described the environment, sediments, and microfauna from both areas plus a portion of the adjacent continental shelf (Fig. 4).

There is a considerable moisture excess for this region (Thornthwaite, 1948; and Fig. 9). This results from many large rivers discharging fresh water into Mobile Bay (Mobile and Tensaw rivers) and Mississippi Sound (particularly the Pascagoula River). The offshore, discontinuous island chain is an effective barrier to ready mixing of this runoff with the open Gulf water (Phleger, 1954). However, some denser, more saline water from the Gulf does enter Mississippi Sound by way of the surge channels and mixes with the fresh water from the rivers within this shallow water body. Thus, there is a steep salinity gradient in bottom waters from the open Gulf (with usually 35°/oo), through the adjacent inlet (near 30°/oo), and into Mobile Bay-Mississippi Sound (to < 5°/oo within 10 miles of the Gulf).

From the foraminiferal distribution data of Upshaw *et al.* (1966, plate 4, reproduced here as Fig. 4), it is evident that the agglutinated Foraminifera are relatively most abundant in water with the lowest salinity values, and that they decrease in relative abundance with increasing salinity. On the other hand, the hyaline calcareous Foraminifera are associated with the more saline Gulf water, diminishing in relative abundance as it is diluted by fresh water within the bay and sound. Representatives of the third group, the porcelaneous Foraminfera, are not found within this restricted area, though they are present (up to 30% or more) in the more saline Gulf water somewhat seaward of the freshwater influence. Hence, the relative abundance distributions of two of the foraminiferal groups are correlated here with water salinity values — hyaline calcareous directly, agglutinated inversely.

TAMPA BAY

Bandy (1956) and Walton (1964) have made ecologic studies of the Foraminifera of Tampa Bay and environs, including Old Tampa Bay (Walton, 1964) and Hillsboro Bay (Bandy, 1956).

Bathymetrically, the bay can be divided into low sand and grass flats of shallow depth (< 15 ft. of water) with superimposed relatively deep channels (Goodell and Gorsline, 1960). Maximum depth in the bay is slightly more than 30 feet, which

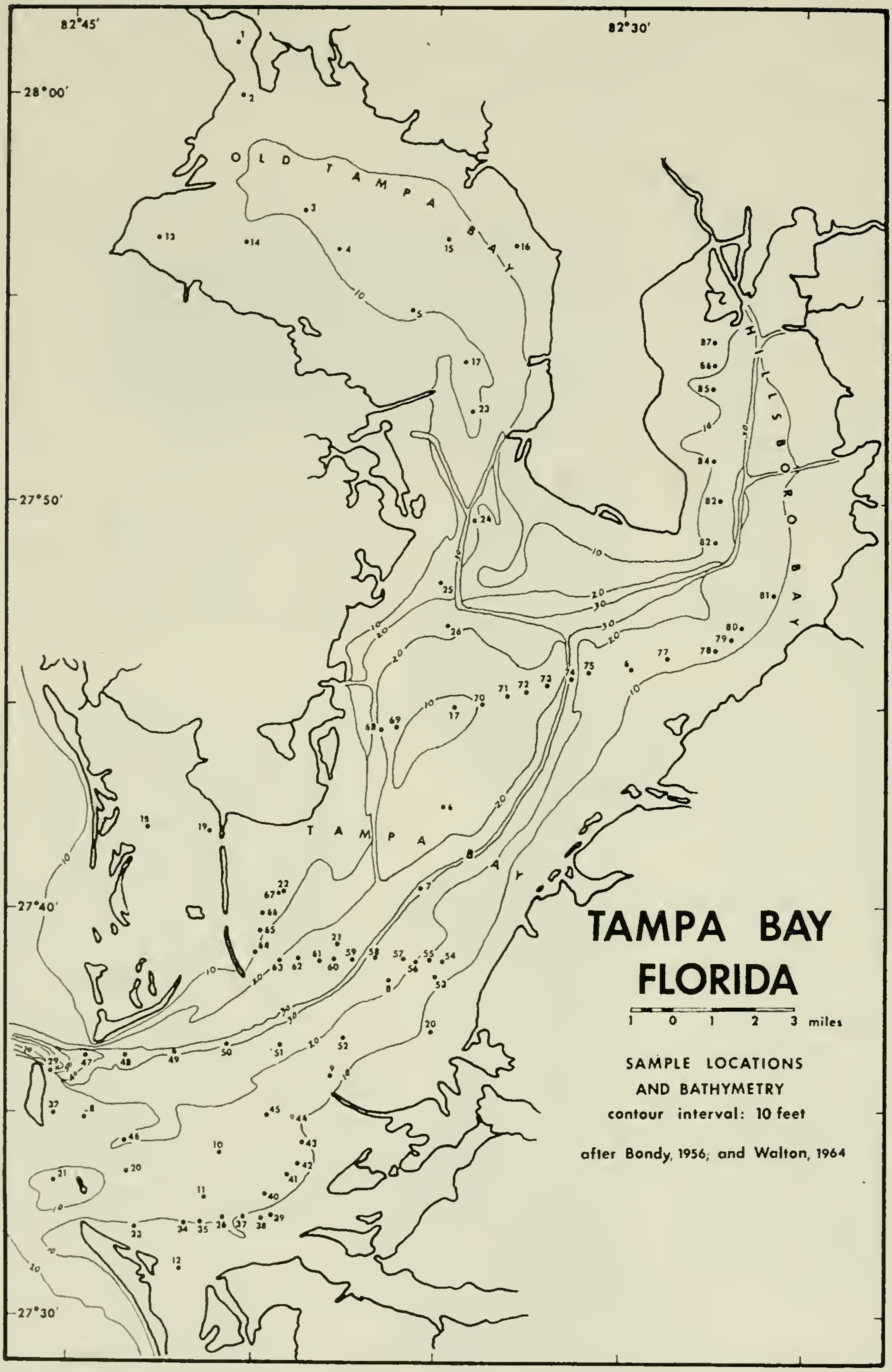
82°45′
82°30′
28°00′
27°50′
27°40′
27°30′
OLD TAMPA BAY
HILLSBORO BAY
TAMPA BAY
TAMPA BAY
FLORIDA
1 0 1 2 3 miles
SAMPLE LOCATIONS
AND BATHYMETRY
contour interval: 10 feet
after Bondy, 1956; and Walton, 1964

Figure 5. Bathymetry and sample locations for Tampa Bay, Florida. (From Bandy, 1956; and Walton, 1964.)

is that of most of the channels (Fig. 5). The sediments of Tampa Bay are predominantly fine to very fine quartz sands (Walton, 1964).

The salinity distribution pattern for Tampa Bay and environs can be qualitatively described as follows: In the channels dissecting the bottom topography, the water salinity is at a maximum near the mouth of the bay complex (somewhat above 'normal' marine), with a very slight gradient to lower salinities in Hillsboro Bay. The adjacent shoal waters have a similar gradient, from near normal marine salinity at the mouth of Tampa Bay to lowest salinities (just slightly above that of river water) in upper Hillsboro Bay. Since the salinity in the channels is everywhere higher than that of the adjacent sand and grass flats, there is also a positive gradient from shallow to deep water.

The relative abundance distributions of the agglutinated and the porcelaneous Foraminifera are shown in Figures 6 and 7, respectively. The changing contributions of these two groups and that of the hyaline calcareous group reflect the salinity gradients just discussed.

These foraminiferal distributions clearly demonstrate a strong correlation between salinity and the relative abundances of each of the three groups. Highest salinity waters characteristically have high percentages of the porcelaneous type associated with them. In successively lower salinities, the hyaline calcareous type and then the agglutinated type reach their maximum relative abundances.

LAGUNA MADRE

Laguna Madre is located within the semi-arid climatic zone of Thornthwaite (1948), and, hence, has a more or less persistent, marked moisture deficiency (Fig. 9). There are no major rivers flowing into the area, and there is only very slight freshwater inflow from ephemeral streams during local rainfall (Rusnak, 1960). The excess of evaporation over precipitation allows the normal marine Gulf waters to enter the shallow basins (average depth, about 2½ ft.) of Laguna Madre and causes the water there to be generally hypersaline. Chlorinities in the northern basin range from 22 to 45°/oo Cl and in Baffin Bay from 1 to 45°/oo Cl; the southern basin, with lower salinities, has up to 35°/oo Cl (Phleger, 1960b).

The temperature of the lagoonal water reflects that of the air (Phleger, 1960b); and because of the positive thermal gradient

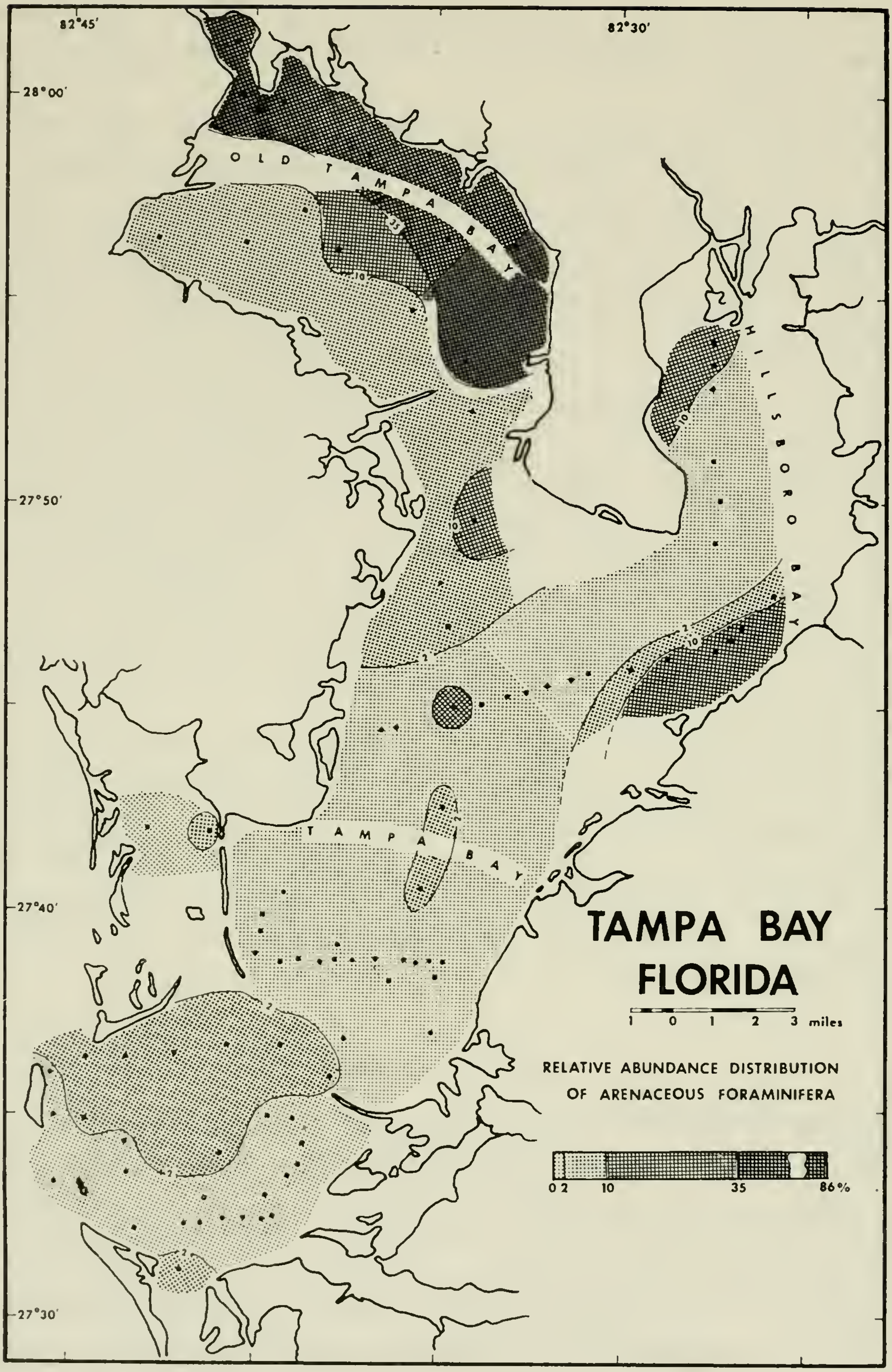
82°45'
82°30'
28°00'
27°50'
27°40'
27°30'
OLD TAMPA BAY
HILLSBORO BAY
TAMPA BAY
TAMPA BAY
FLORIDA
1 0 1 2 3 miles
RELATIVE ABUNDANCE DISTRIBUTION
OF ARENACEOUS FORAMINIFERA
0 2 10 35 86%
2
10
35

Figure 6. Relative abundance distribution of agglutinated Foraminifera from Tampa Bay, Florida. (Data from Bandy, 1956; and Walton, 1964.)

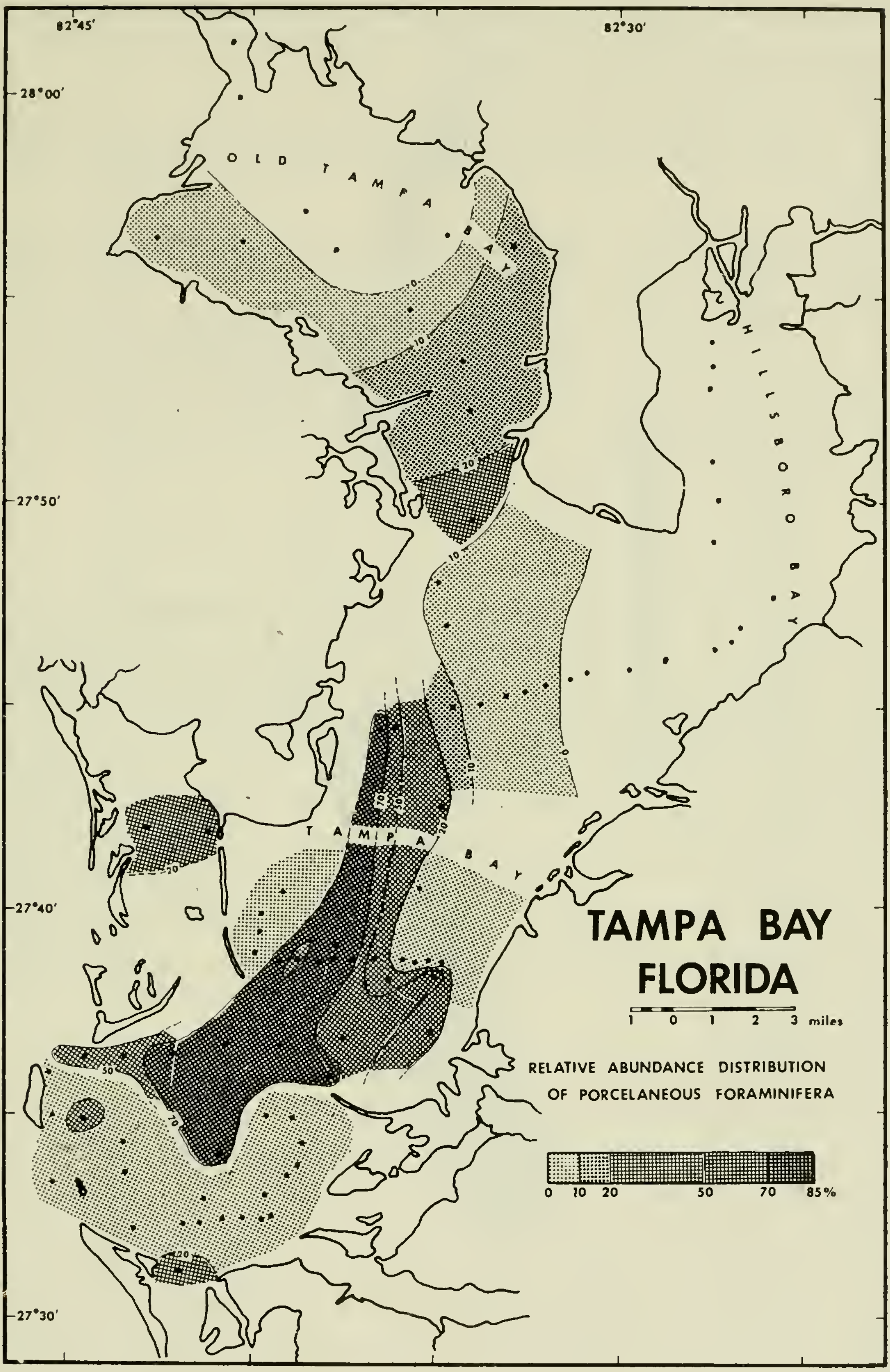
82°45'
82°30'
28°00'
27°50'
27°40'
27°30'
OLD TAMPA BAY
HILLSBORO BAY
TAMPA BAY
TAMPA BAY
FLORIDA
1 0 1 2 3 miles
RELATIVE ABUNDANCE DISTRIBUTION
OF PORCELANEOUS FORAMINIFERA
0 10 20 50 70 85%

Figure 7. Relative abundance distribution of porcelaneous Foraminifera from Tampa Bay, Florida. (Data from Bandy, 1956; and Walton, 1964.)

in this area from north to south (Espenshade, 1960), the relative abundance distribution of the foraminiferal groups can be correlated with this parameter.

The foraminiferal populations are dominated by the porcelaneous types in nearly all samples studied (Phleger, 1960b) (Fig. 8).

In Laguna Madre, the foraminiferal distributions are related to both salinity and temperature. Low salinity areas (Baffin Bay) are dominated by hyaline calcareous species; high salinity areas by porcelaneous species. But within the hypersaline environments, the relative proportions of the two types are correlated with temperature — porcelaneous (most abundant in the southern basin) directly, hyaline calcareous inversely.

General Discussion of the Distributions

I have shown that the relative abundance distributions of the three groups of benthonic Foraminifera are closely related to salinity distributions, and occasionally to temperature gradients, within several shallow-water environments adjacent to the Gulf of Mexico. The relationship on a *local* scale shows a gradient of maximum relative abundances for the three groups, from agglutinated forms in low salinity waters, to hyaline calcareous forms in waters of intermediate salinities, to porcelaneous forms in waters of highest salinity. Each of the various types does not necessarily dominate the fauna at its maximum, but only reaches its peak relative abundance there for the bay or estuary under consideration.

Some modifications to this sequence occur. Most can be explained as the simple displacement of either or both of the end-member groups — the agglutinated and the porcelaneous types — from the sequence. Thus, for example, in the Mobile Bay-Mississippi Sound environment, the porcelaneous forms are not present, and the sequence ends with the hyaline calcareous maximum. However, at the opposite end of the spectrum, the agglutinated types not only reach their maximum, but completely dominate the upper bay fauna to the exclusion of any calcareous forms. This situation is correlated with a much higher runoff and consequent lower salinity for this estuary than for most of the others.

On the other hand, the samples from Laguna Madre yielded almost no agglutinated Foraminifera while the hyaline calcareous forms reach their maximum abundance in waters of the lowest

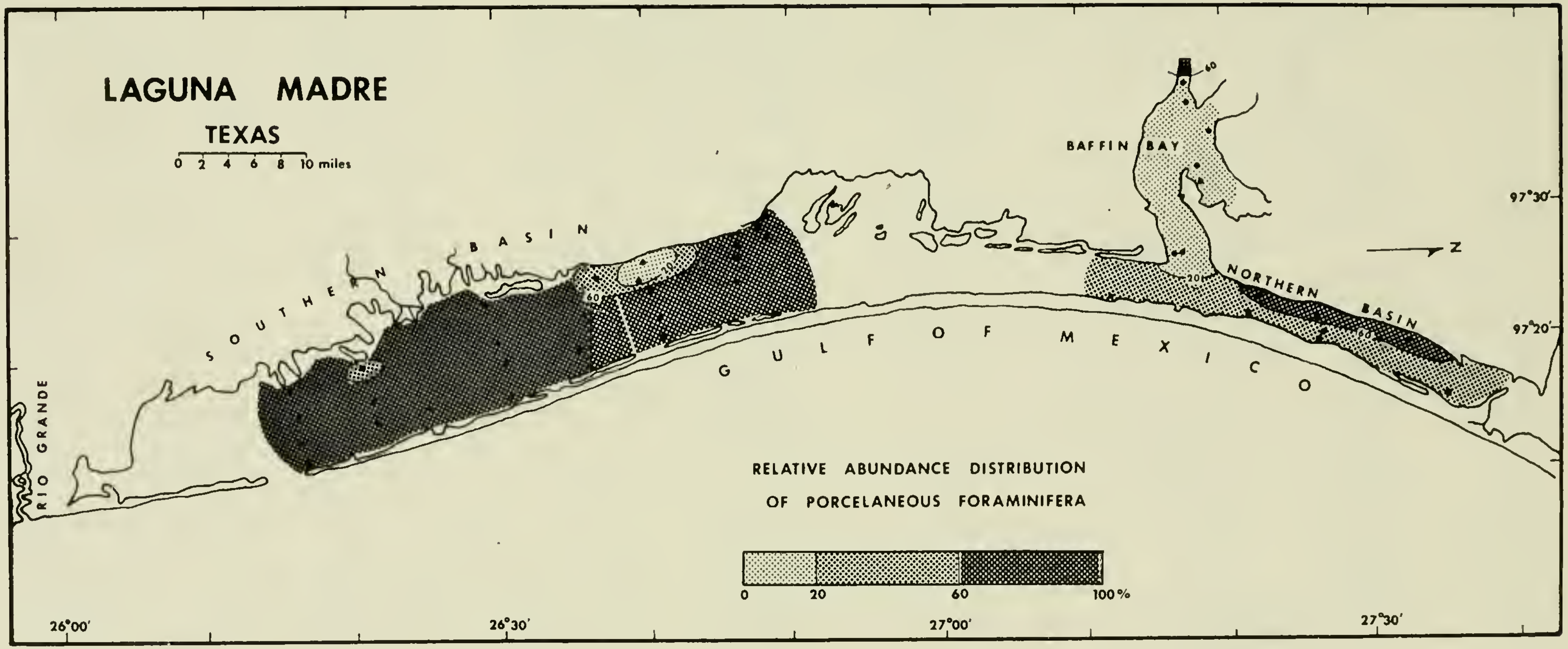
LAGUNA MADRE
TEXAS
0 2 4 6 8 10 miles
RIO GRANDE
SOUTHERN BASIN
60
BAFFIN BAY
60
20
NORTHERN BASIN
60
N
GULF OF MEXICO
97°30′
97°20′
RELATIVE ABUNDANCE DISTRIBUTION
OF PORCELANEOUS FORAMINIFERA
0
20
60
100%
26°00′
26°30′
27°00′
27°30′

Figure 8. Relative abundance distribution of porcelaneous Foraminifera from Laguna Madre, Texas. (Data from Phleger, 1960b.)

salinity and temperature. Thus, the sequence is still preserved, but with one end-member excluded. This area is characterized by higher than "normal" marine salinities and by high temperatures.

Intermediate faunal and environmental situations are present and, as might be expected, are located geographically between these end-member dominances. Matagorda Bay and environs is a good example of these conditions. The foraminiferal fauna is everywhere dominated by the hyaline calcareous types, to the near exclusion of agglutinated and porcelaneous types. This can be correlated with intermediate regional temperatures and with the close balance of run-off plus precipitation against evaporation, the latter of which produces a salinity near the normal value for the open Gulf in that region (which is slightly below "normal" marine; cf. Fig. 3).

This sequence in maxima of the relative abundances of the three groups of Foraminifera is present not only on a *local* scale within a bay or lagoon, but also on a *regional* scale, across the entire northern Gulf of Mexico. Just as on a local scale, the trend is correlated with salinity and with temperature.

There are two regional trends in the environment (or climate) which we must recognize. These are: 1) the gradual increase in *temperature* from north to south; and 2) the gradual shift in *moisture budget* from a marked surplus in the Mississippi Delta region, westward through a moisture balance near Matagorda Bay, to a marked moisture deficit in the region about Laguna Madre, and eastward to a near balance, but definite surplus, along most of the Florida coast.

The relative abundance distributions of the three groups of benthonic Foraminifera together with isotherms of the January normal temperature and with the moisture budget zones (after Thornthwaite, 1948) of the coastal region of the northern Gulf of Mexico have been summarized in Figure 9. The sequence in maxima of relative abundances of the Foraminifera, correlative with a sequence of environmental factors, can be seen as a regional continuum from Mobile Bay, along the Louisiana and Texas coasts, to Laguna Madre. The Mobile Bay foraminiferal fauna is dominated, for the most part, by agglutinated species. This is correlated with excessive moisture and consequent low salinity water within the bay. In addition to this, mean annual temperatures are here near the lowest for the Gulf area.

Sabine Lake, the next area of study to the west, again has a fauna dominated by agglutinated species (Kane, 1967) and is

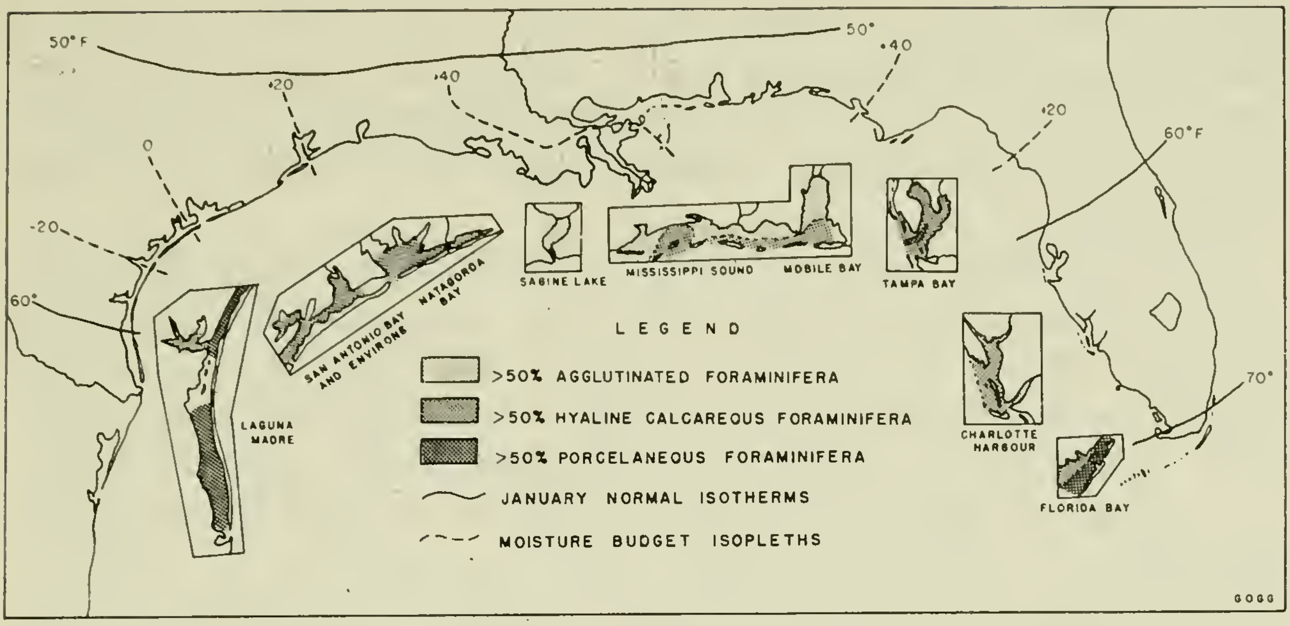
50°F
50°
•40
•20
•40
0
•20
-20
60°F
60°
70°
SABINE LAKE
MISSISSIPPI SOUND
MOBILE BAY
TAMPA BAY
MATAGORDA BAY
SAN ANTONIO BAY AND ENVIRONS
LAGUNA MADRE
CHARLOTTE HARBOUR
FLORIDA BAY
LEGEND
>50% AGGLUTINATED FORAMINIFERA
>50% HYALINE CALCAREOUS FORAMINIFERA
>50% PORCELANEOUS FORAMINIFERA
JANUARY NORMAL ISOTHERMS
MOISTURE BUDGET ISOPLETHS
GOGG

Figure 9. Dominance of agglutinated, hyaline calcareous, and porcelaneous Foraminifera in the northern Gulf of Mexico paralic environments; including January normal isotherms after Espenshade (1960), and moisture budget isopleths after Thornthwaite (1948).

included, essentially, within the same environmental zones as Mobile Bay. The moisture surplus is actually less than in the previous area, but this is compensated by the greater restriction from mixing with the open Gulf.

To the southwest, Matagorda Bay and environs is within a warmer climatic zone and is also within a zone of only very slight moisture surplus. Emphasizing this lower moisture surplus is the lack of large rivers discharging fresh water into the bay. The result is relatively warm water with salinities near, but somewhat less than, those of the adjacent Gulf. Commensurate with this rise in water temperature and salinity over that of Sabine Lake and Mobile Bay is a shift in the foraminiferal fauna. Here the hyaline calcareous forms dominate (Lehmann, 1957; Shenton, 1957).

San Antonio Bay and environs displays an anomalous, but explicable, reverse in the environmental and faunal sequence (Parker, Phleger, and Peirson, 1953; Phleger, 1956; Shepard and Moore, 1955 and 1960), despite its position within the climatic trend to higher temperatures and greater moisture deficiency. The influx of fresh water to the bays from the relatively large San Antonio-Guadalupe River system is the cause of the much lower water salinity values here than in Matagorda Bay, which is in a general area of greater moisture surplus. There is a correlative shift in the foraminiferal fauna to one dominated in the upper bay by agglutinated forms. The central and lower bay fauna is dominated by hyaline calcareous forms as in Matagorda Bay, but there is still a higher proportion of agglutinated types in the former area, commensurate with the lower average salinity there.

Laguna Madre, in a climatic zone of high annual temperatures and marked moisture deficiency, completes the faunal sequence observed on a smaller scale in some of the bays around the Gulf. Agglutinated Foraminifera are virtually absent from all samples taken in the lagoon (Phleger, 1960b). In the northern basin of the lagoon, the proportion of hyaline calcareous specimens is slightly less than that of porcelaneous. And the porcelaneous types overwhelmingly dominate the southern basin. Hence, there is a direct correlation between temperature and the proportion of porcelaneous forms in the bottom sediment.

An environmental continuum and faunal dominance sequence similar to that just described can be documented for the Florida Gulf coast and correlated with climatic trends from Mobile Bay to Florida Bay. The change in moisture budget is not so dramatic as to the west, as a surplus is maintained along the entire coast to the tip of Florida (Fig. 9). However, the temperature gradient is even steeper, making Florida Bay approximately 6°C warmer than Laguna Madre during January, though both are at comparable latitudes.

The sequence in maxima of relative abundances of the three benthonic groups is developed and can be correlated with the general environmental trend to higher salinities and higher temperatures to the south. After Mobile Bay, with its overwhelming dominance of agglutinated Foraminifera, the next area to the south is Tampa Bay. The whole foraminiferal sequence is developed here, but the hyaline calcareous types dominate the fauna over the greater part of the bay, except in the deep channels. Charlotte Harbour and vicinity has a similar fauna, largely dominated by hyaline calcareous forms (data after Bandy, 1954), though the whole sequence is again present. Both of these areas are similar environmentally and climatically. Both are in the wet subhumid zone and both receive limited drainage from the surrounding, low-lying, karst topography. There is some difference in latitude and hence, in mean annual temperature, but this is minimal. Thus, the two areas have very similar foraminiferal faunas.

The fauna of Florida Bay is dominated in the near-shore, lower salinity areas by hyaline calcareous types, and by porcelaneous types seaward, toward the keys (Lynts, 1962). This faunal composition is similar to that of Laguna Madre, but with a slightly greater proportion of hyaline calcareous types. Thus, despite its location within a wet subhumid climatic zone (Fig. 9), comparable in this respect to Matagorda Bay, it has a fauna similar to that of a lagoon within a semi-arid zone. Matagorda Bay and Florida Bay both have only very small rivers emptying into them. The differences between Florida Bay and Matagorda Bay, and the similarities that the former has with Laguna Madre can perhaps be explained on the basis of salinity of adjacent Gulf water, and on the basis of temperature.

The salinity of the open Gulf water replacing that evaporated from Florida Bay is somewhat higher than that entering Laguna Madre, and considerably higher than that available to Matagorda Bay (Fig. 2). Mean annual temperature at Florida Bay is somewhat higher than at Laguna Madre and considerably higher than at Matagorda Bay (Fig. 9). Thus, though the water of Florida Bay is diluted by runoff and precipitation similar to that for Matagorda Bay, it can be more quickly reconstituted to a higher salinity owing to greater evaporation and easier mixing with waters more saline than "normal" marine. It is also possible that the high proportion of porcelaneous Foraminifera should be correlated with the higher temperatures there, as I postulated for Laguna Madre.

To summarize the distributions and correlations discussed in this section, the following conclusions can be drawn. On a *local scale, i.e.,* within a bay, lagoon, or other shallow-water environment, there is a succession of relative abundance maxima from agglutinated, through hyaline calcareous, to porcelaneous types; this is correlated with a trend in salinity or temperature values from low to high for the area. Also, either or both of the end-member types can be displaced from the sequence with commensurate shifts in the salinity and temperature gradients. These gradients are the most obvious factors of the environment to which the faunal sequence can be related. There are essentially uniformly shallow depths over most of the areas, and no apparent correlation of the faunal groups with bathymetry. Where several different sediment types are present within a single bay area, they are generally correlated with depth and, hence, not correlated with the fauna. In some areas, such as Florida Bay and Laguna Madre, a relative abundance sequence in the foraminiferal types is correlated with the temperature or salinity gradient in each bay despite the uniformity of bottom sediment type.

Regionally, the same foraminiferal sequence is present — manifested in the various types dominating the population from bay to bay in succession. This sequence is again correlated with a general trend in salinity and temperature. This trend in the shallow-water environmental continuum is explicable in terms of climate and physiography of the adjacent coastal plain. The main climatic factors necessary for explanation are moisture balance and temperature. The influence of physiography on the local environment is evident in the amount of runoff carried into the various areas of investigation.

Environmental Factors Controlling Distribution of Foraminifera

I present the hypothesis that the actual environmental factor controlling the distribution of Foraminifera is the *availability of calcium carbonate* (dependent, to a great extent, on salinity, temperature, and depth of water); or the ease with which these one-celled organisms can extract and precipitate $CaCO_3$ for their test from the surrounding water.

Chemistry. Revelle (1934), in discussing the physico-chemical factors affecting the solubility of calcium carbonate in seawater, stated that, from the mass law equation $Ca^{++} \times CO_3^{--} = {}^{K}CaCO_3$, three parameters control the solubility of $CaCO_3$: concentrations of calcium and carbonate ions and the value of the temperature-dependent constant ${}^{K}CaCO_3$. "These factors are in turn dependent on salinity, temperature, hydrostatic pressure due to depth below the surface, carbon dioxide content, and the concentration of hydrogen and hydroxyl ions, as indicated by the *p*H" (Revelle, 1934: 103–104). Revelle and Fairbridge (1957: 256) conclude that the two most important processes facilitating the precipitation of calcium carbonate probably are: (1) an increase in temperature, which lowers the solubility of CO_2, thus increasing the carbonate ion concentration; and 2) evaporation, which increases the calcium ion concentration and carbonate alkalinity.

These two processes, governing the carbonate ion and calcium ion concentrations, respectively, can be equated with increasing temperature and increasing salinity. Thus, in low salinity and low temperature environments calcium carbonate will not be easily precipitated, owing to low calcium and low carbonate ion concentration, the latter being largely a result of increased solubility of CO_2 in the water. On the other hand, waters with high salinites and high temperatures, with their relatively high calcium and carbonate ion concentrations, are saturated or supersaturated with respect to calcium carbonate, as in tropical and subtropical surface seawater (Chave and Schmalz, 1966). In these areas calcium carbonate will be precipitated most readily.

Thus, all of the environmental parameters tend to increase the availability of calcium carbonate from the Mississippi Delta region toward the Rio Grande on the west, and toward Florida Bay on the east. This trend is closely correlated with the observed trend in relative abundance distributions of the foraminiferal groups studied (see Fig. 9 for a summary of climatic factors and the foraminiferal distributions).

From these observations, it is apparent that agglutinated Foraminifera are relatively most abundant in areas with the lowest availability of calcium carbonate. Porcelaneous Foraminifera, on the other hand, are associated with high availability of calcium carbonate, and often dominate the foraminiferal faunas of warm, saline tropical or subtropical waters. Finally, the areas characterized by intermediate calcium carbonate availability are dominated by the hyaline calcareous Foraminifera. This generalization is true on nearly all scales of observation: within a bay or lagoon, among several adjacent bays of a region, on contiguous portions of the continental shelf (Greiner, 1970), and on a worldwide scale.

Mechanism. The agglutinated Foraminifera do not require the precipitation of calcium carbonate in construction of their tests. They utilize the available sediment grains, cementing them together with a predominantly organic material (Hedley, 1963; Towe, 1967). They are therefore free of restriction to any of the marine or estuarine environments. The calcareous Foraminifera (both hyaline calcareous and porcelaneous), on the other hand, require calcium carbonate for the construction of their tests. The extent to which its availability is required depends upon the ability of the organism to concentrate and secrete (or allow precipitation of) calcium carbonate against (or within) the chemical environment of the water. I suggest that a fundamental distinction between the hyaline calcareous and the porcelaneous Foraminifera lies herein.

Electron microscope studies (Hay, Towe, and Wright, 1963; Towe and Cifelli, 1967; Lynts and Pfister, 1967) have shown that there is a radical difference between the shell structure of porcelaneous Foraminifera and that of the hyaline calcareous types. In the porcelaneous wall there is a thick, inner layer with a three-dimensionally "random" array of elongate crystals and a pavement-like, surface veneer that in part exhibits preferred orientation. The hyaline calcareous wall, on the other hand, is made up of calcite crystals with a preferred orientation, the whole wall being penetrated by numerous pores, which are visible under the light microscope as well (Towe and Cifelli, 1967). These observations are consistent with the general separation (Loeblich and Tappan, 1964) of the hyaline calcareous and the porcelaneous wall types on the basis of perforations of one type and porcelaneous appearance of the other.

Lynts and Pfister (1967) have pointed out the differences in crystallization of the wall as observed for these two test types. One species with a hyaline calcareous wall was observed in the process of chamber formation (Angell, 1967a and b). The foraminifer, when beginning to add a new chamber, extended a portion of its protoplasm through the aperture of the test, forming a bulbous drop with the exact shape of the prospective chamber. An organic sheath formed on the surface of the drop. Shortly thereafter, protoplasm was again exuded (through the new aperture in the organic sheath) and covered, in a thin film, the surface of the new, tectinous chamber wall. Calcite crystals were then observed to nucleate on the organic surface and to grow upward (perpendicular to the surface) within the exuded cytoplasm, until the calcareous wall was complete. Observations by Towe and Cifelli (1967) suggest that other hyaline calcareous species also nucleate calcite crystals for test formations on an organic base.*

Arnold (1964), while observing chamber formation of a porcelaneous species (similar to that of hyaline calcareous types up to the secretion of calcite), noted that the calcite crystals grew in "random" fashion within the organic matrix formed by the exuded cytoplasm of the protist, not upon an organic nucleating surface (see Fig. 10 for a diagrammatic comparison of crystal growth in the two types). Lynts and Pfister (1967) have pointed out this difference between these two test types, and Towe and Cifelli (1967), likewise, conclude that porcelaneous wall structure is significantly different from hyaline calcareous.

I suggest that the absence of a nucleating surface for the se-

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*Subsequent work by Towe (1972) suggests that this may not be true for all Foraminifera in this group.

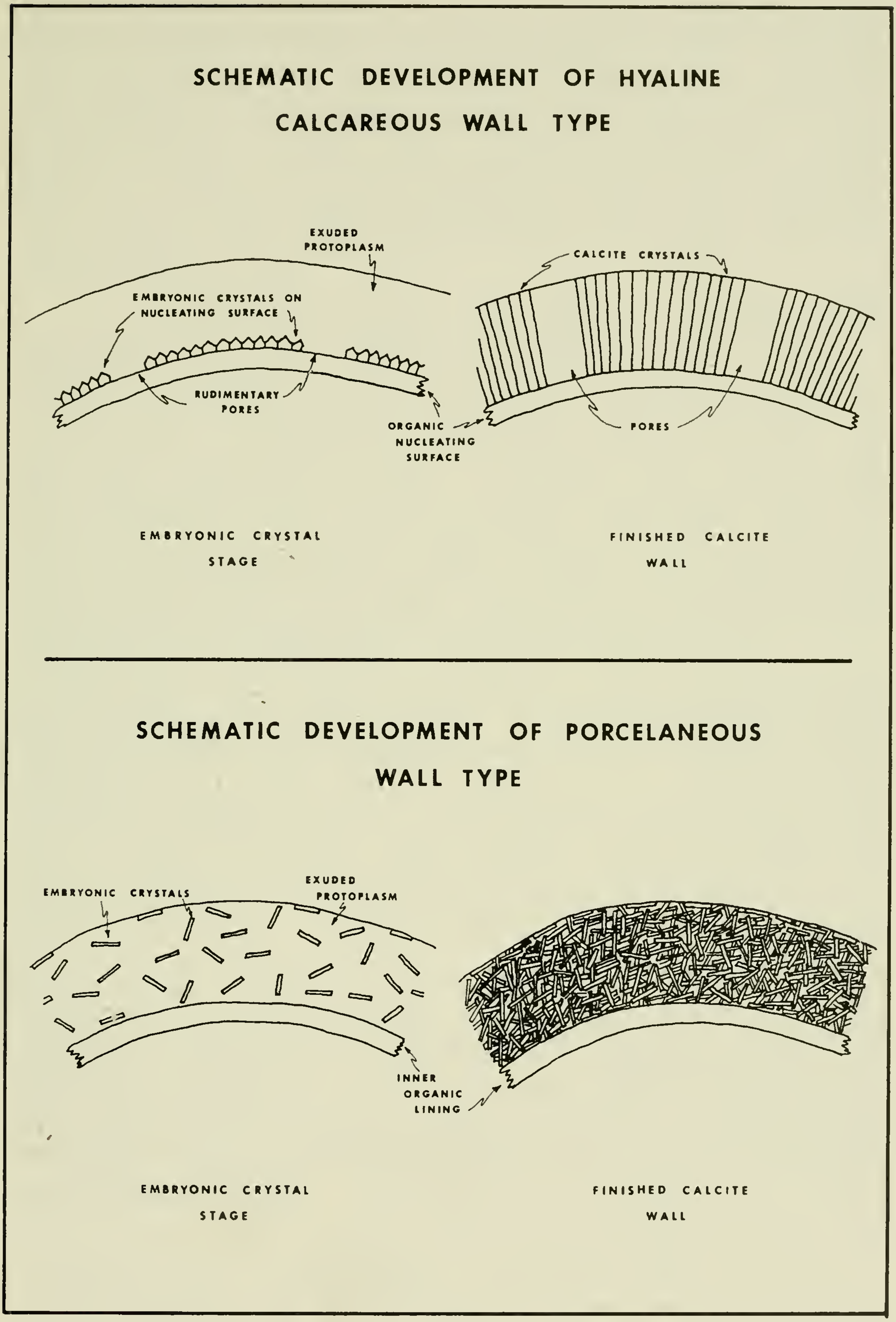
SCHEMATIC DEVELOPMENT OF HYALINE CALCAREOUS WALL TYPE
EXUDED PROTOPLASM
EMBRYONIC CRYSTALS ON NUCLEATING SURFACE
RUDIMENTARY PORES
ORGANIC NUCLEATING SURFACE
CALCITE CRYSTALS
PORES
EMBRYONIC CRYSTAL STAGE
FINISHED CALCITE WALL
SCHEMATIC DEVELOPMENT OF PORCELANEOUS WALL TYPE
EMBRYONIC CRYSTALS
EXUDED PROTOPLASM
INNER ORGANIC LINING
EMBRYONIC CRYSTAL STAGE
FINISHED CALCITE WALL

Figure 10. Diagrammatic sketch illustrating differences in test wall calcification in porcelaneous and hyaline calcareous Foraminifera. See text for discussion.

cretion of calcite by the porcelaneous Foraminifera dictates that they live within an environment of readily available calcium carbonate — at the point of "saturation" or even "supersaturation."** The nucleating surface employed by the hyaline calcareous Foraminifera, however, allows them a greater range of habitable environments. Because of this, they can do well both in normal marine and in slightly hypersaline conditions, and are prevented from thriving only within areas of low calcium carbonate availability (usually low salinity) and areas of "hyper-supersaturation" (see below for further discussion).

In the very low salinity environments, where the availability of calcium carbonate is below the threshold required by hyaline calcareous forms, the agglutinated Foraminifera will predominate. This is so simply because the agglutinated species are not restricted by such a boundary, while the calcareous types are. As waters with more readily available calcium carbonate are approached, more hyaline calcareous forms will be present, thus diminishing the relative abundance of agglutinated types. Though the agglutinated types are not excluded from environments of high calcium carbonate availability, they are subordinate in abundance to the calcareous forms there. This can be explained by the ability of calcareous forms to diversify and occupy ecological niches not as readily available to the agglutinated types (*e.g.*, marine plants), as the construction of an agglutinated test ties the protist to its source of raw material — the bottom sediments. (Again, this is a relative situation. I am aware that some agglutinated types may live on marine plants utilizing the fine sediment dust that clings to their surfaces for test construction.)

The porcelaneous types reach their maximum relative abundance under environmental conditions of maximum availability of calcium carbonate — the tropics and subtropics with high temperatures and hypersalinities. Their proportion of the total fauna decreases in the direction of lower calcium carbonate availability, toward lower temperatures as in Laguna Madre, or toward lower salinities as in Florida Bay. This is so because they have greater difficulty in secreting calcite in these environments,

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**I use the terms "saturation," "supersaturation," and "hyper-supersaturation" in a *relative* sense. Though these terms do have definite meanings in chemistry, it is difficult to say at what point a sea-water solution is "saturated" with respect to $CaCO_3$ in a natural environment, and even more difficult to state the relation of the foraminiferids to some precise value of saturation. They can be related relatively, however.

while the hyaline calcareous types are seemingly not hindered in this process until very low salinities or temperatures are reached. The porcelaneous types can completely dominate the fauna in environments of very high calcium carbonate availability owing, perhaps, to the unordered crystalline nature of their test walls. Hyaline calcareous types would perhaps be unable to secrete well-ordered crystals in an environment of calcium carbonate "hyper-supersaturation."

Consequently, Foraminifera with hyaline calcareous walls reach their maximum relative abundance in areas of intermediate calcium carbonate availability, where the porcelaneous types are greatly diminished owing to problems of calcite secretion.

Summary. An hypothesis has been proposed to explain the observed foraminiferal sequence correlated with salinity and temperature gradients within estuarine environments. The environmental factor thought to control the distributions of major groups is the availability of calcium carbonate utilized in test construction by two of the types. This factor is dependent mainly on temperature, salinity, and CO_2 content of the water.

This hypothesis adequately explains the observed distributions of these groups; it explains, through physiologic interaction with the environment, the correlation between foraminiferal groups and temperature and salinity gradients; and it ultimately explains the correlation of these groups with climatic factors. The fact that this correlation exists between the foraminiferal sequence and the environmental factors reducible to calcium carbonate availability, and the fact that this relationship can be explained by varying abilities of the foraminifers to construct tests suggest, that these organisms secrete calcite in near-equilibrium with their environment. This implies, further, that these protists are unable to concentrate and precipitate calcium carbonate from the seawater in very great chemical opposition to their surroundings and that they are, in this sense at least, simple organisms, dependent on, and controlled to a great extent by, their environment.

Geologic Significance of Results

The understanding of environmental effects on the distribution of organisms and on the modification of phenotypes is essential to the interpretation of paleoenvironments. The purpose of this study has been to gain some understanding of factors governing the distribution of Foraminifera in Recent environments. The difficulty in learning the causes of distribution of any particular *species* is apparent, and geologic applicability of such knowledge is severely limited by the geologic range of the species. In this light, I have sought to determine the environmental control on a characteristic of the fauna that transcends the specific level of classification and which is amenable to paleoecologic extrapolation. I have shown that Foraminifera are distributed within the Recent environment in a fashion covariant with certain factors summarized as the availability of $CaCO_3$. The proposition that the availability of $CaCO_3$ is indeed the cause of their relative abundance distribution is supported by a credible explanation, on the physiologic level, of foraminiferal test construction.

The understanding of distributions at this level depends only on a knowledge of the wall types, not on individual characteristics of a taxonomic group. Much can be learned concerning salinity and temperature distributions in ancient seas and estuaries through use of Foraminifera at this morphologic level. With a more thorough understanding of the causes of planktonic distributions and changes in foraminiferal diversity on the continental shelf, more can be learned of paleobathymetry and location of shore-lines.

Since work with the Foraminifera at this level circumvents the problems associated with extending interpretations of various Recent taxa back in time, application of the principles gained can be extrapolated through the Mesozoic to the beginnings of the calcareous Foraminifera. One major assumption must be made for the interpretation of fossil faunas. This is that the ability of Foraminifera to secrete calcite for particular wall types within a given environment of $CaCO_3$ availability has not changed appreciably since the corresponding development of each test type. This assumption, it would seem, is a fair one; if the crystalline structure within the wall of Jurassic porcellaneous Foraminifera is similar to that found in Recent specimens of that wall type, it is reasonable to assume that the physiologic processes that produced it were similar.

Perhaps a more important inference can be drawn from the results of this study. If the Foraminifera depend to such an extent on the availability of $CaCO_3$ in specific degrees of saturation or supersaturation within the environment for secretion of their tests, then they cannot readily concentrate these ions physiologically and hence cannot easily act in chemical opposition to their surroundings. This implies further that other aspects of foraminiferal tests are subject to simple control by the environment. I suggest that such factors as general test morphology, apertural position and number, and chamber number may be governed not strictly genetically (as is implied by the erection of specific or generic groups based on these characters), but by the macro- or microenvironment of the living individual. This, then, is an open avenue for research. If environmental causes for various morphological characteristics can be derived, immeasurable paleoecologic value can be attributed to Foraminifera.

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Appendix

On the Construction of Calcite Walls in Foraminifera

The living calcareous Foraminifera have been divided into two suborders on the basis of general test wall construction: the Miliolina have nonporous, porcelaneous walls; the Rotaliina have a glassy appearance, and are penetrated by numerous pores. Studies with the electron microscope have upheld this basic distinction and have revealed the crystal arrangements underlying and producing this difference, as seen by the light microscope.

The miliolid test wall is composed of two layers of calcite rhombs or needles: an inner, "randomly" oriented layer (which is the thicker) and an outer, pavement-like layer, one rhomb thick, with the rhombs oriented parallel to the surface. The crystallization process in miliolid foraminifers has been observed and reported by Arnold and by Lynts. The process is as follows: Cytoplasm is extruded through the aperture; it then takes on the form of the new chamber. A layer of fibrous organic matter is deposited on the surface of the chamber and will become the "inner organic lining" of the test. After the new aperture is formed, cytoplasm is again extruded, but this time it covers the new chamber in a thin organic sheath, which is to act as the crystallizing matrix.

Mineralization then occurs in two waves of crystal growth, with the rhombs being nucleated either spontaneously or by properly patterned organic molecules, but at many "randomly" placed sites throughout the sheath of matrix. This results in growth of the crystals in a *nonoriented* fashion within an immiscible solvent. This will be contrasted with the result of *oriented* crystal growth in the rotaliids.

Thus the randomly oriented rhombs in the inner layer are the result of randomly oriented crystal nuclei. What special mechanism operates to orient the surface rhombs? I believe this is simply the result of surface tension at the protoplasm-seawater interface, acting on the elongated crystals to align them parallel to that surface. No biological directives are required; it is a simple, physical process. No special crystallizing mechanisms should be sought, and no adaptive significance can be attached to this pavement-like surface layer.

The mineralization process in a hyaline calcareous foraminifer has been watched and reported by Angell, and a mechanism for this process has been proposed by Towe and Cifelli on the basis of the electron microscopic study of test wall sections. The process is as follows: Cytoplasm is extruded through the aperture, and takes on the shape of the chamber to be formed. A fibrous organic layer is secreted to cover the chamber. The cytoplasm is again extruded through the new aperture and covers the new chamber in a thin organic sheath. To this point the process is similar to that of the miliolids, but the fibrous organic layer, which was merely an inner lining for the miliolid, has taken on a new function. It apparently acts as a template for calcite nucleation. Crystallization then takes place beginning on this template, with the calcite crystals growing upward within the organic sheath. When the process is completed, there are crystals and pores oriented perpendicular to the test surface.

It is my opinion that these pores and crystals are simply the result of oriented crystallization of two immiscible substances from an originally miscible solution — the cytoplasmic sheath. My analysis of the process is as follows: The entire fibrous surface of the new chamber can act as a nucleation template. However, as crystallization commences, both calcite and organic matter are coming out of solution. Since these are immiscible as solids, there will be separation of the two phases. Organic matter will be excluded from the calcite crystal lattice and will migrate toward, and collect in, relatively equally spaced organic plugs on the template surface (the "pore processes" of Angell). As crystallization continues, the same process will result in the upward growth of the two separated phases: calcite will continue to crystallize on calcite, and organic matter on the pore processes. The final result is a wall with oriented calcite crystals, penetrated by organic plugs, which upon death and decay will leave the characteristic "pores" of the hyaline calcareous foraminifers.

The results of the same process can be observed on a macroscopic level, and in an even more convincing manner, in your home refrigerator. Most ice cubes exhibit "pore" structures amazingly similar to those of the hyaline calcareous Foraminifera. They are formed by the entrapment of gases formerly dissolved in the water, which must come out of solution during crystallization. If freezing proceeds from the top down, the gas cannot escape into the atmosphere, and space within the cube must be provided. As crystallization proceeds the water becomes saturated with the gas, and as it comes out of solution, it tends to gather into bubbles at more or less equally spaced sites at the ice surface. This, I am suggesting, is analogous to the separation and collection of organic matter into the "pores" of foraminiferal walls during their mineralization.

The total volume of pore space in the ice cube is dependent on the amount of dissolved gas at the onset of crystallization, but the pore size and density is related to rates of crystallization, as indicated by a few simple experiments which I conducted. The faster the cooling rate of the ice, the smaller, and hence more closely spaced are the pores. This is reasonable, as greater migration of the excluded molecules is possible with slower cooling.

The extension of the original bubbles, and hence the elongation of the pores, is the result of simple physical processes. As crystallization continues ice will tend to extend already-existing ice crystals, and the gas will collect at sites already occupied by gas. When the entire solution is used up, crystallization stops and the analogy is complete.

Thus "pores" are developed in the crystallization of ice without the need of biologically derived genetic directives, and, I suggest, the same mechanism operates in the calcification of foraminiferal walls. Surely no "adaptive significance" can be ascribed to ice cube pores. Likewise, I believe we err in searching for a "purpose" in the construction of foraminiferal pores. I think the pores are simply the result of the simultaneous crystallization of two immiscible substances upon a nucleation template. Pores do not develop in the porcelaneous walls because nucleation of the calcite crystals is at many sites, scattered throughout the matrix, and exclusion of organic matter from the lattice during crystal growth is accomplished by merely pushing it aside; whereas, in the rotaliid wall, calcite is being nucleated over an entire surface, necessarily forcing the organic matrix to gather at particular sites. Thus, it was the mode of calcification, the organic nucleating surface, which was selected for, and which has adaptive significance, not the "pores." However, this does not exclude the possibility that foraminifers use these "pores" in the quest for specialized adaptations. By increasing the ratio of organic matter to $CaCO_3$ (quite possibly through genetic control), it is possible to reduce the calcite wall to a mere lattice work composed almost entirely of pore space, as in the genus *Globigerinoides,* thereby lightening the test in preparation for a planktonic habit. Thus, the very enlarged pores of *Globigerinoides* are in a close-packed condition resulting in hexagonal openings and consequent intervening small triangular calcite pedestals serving as bases for the growth of the spines characteristic of this genus. The spine growth can be simply ascribed to the continued crystallization of calcite in the direction it was started — a common phenomenon in crystal growth.

The factors of pore density and total porosity in recent planktonic Foraminifera have been studied by Bé and are found to be related to environment in a gross way. I suggest that *total* porosity will be related to some factor or factors that govern the matrix to calcite ratio (perhaps this is entirely genetic) and that pore size and density will be found to be related to factors governing rates of crystallization. And this might more closely correlate with environmental parameters. Perhaps in areas of $CaCO_3$ supersaturation crystallization will be most rapid, resulting in many, minute pores spread over the test, as opposed to larger, more widely spaced pores that might be found in regions of environmentally controlled slow rates of crystallization.

In summary, I would like to emphasize that this is purely a hypothesis for pore formation based on other hypotheses for calcification mechanisms in Foraminifera, and quite possibly the whole matter is more complex than what I have presented here. However, I believe it is important to refresh our thinking by coming to problems from new angles, by making analogies in the biological world with things or processes in the purely physical or chemical world. I especially think that Foraminifera are much less complicated biologically than most workers currently suppose. Much of their activity, their feeding, their shell construction can be duplicated in completely nonbiological systems. Much of their shell morphology is predictable from a purely geometrical point of view; for example, consider the stacking of different sized spheres. Thus, in my opinion, Foraminifera, perhaps more than any other group of organisms, can be utilized in paleoecological studies, because they are basically simple physicochemical systems; they do not exert much biological pressure against the environment, and hence they are closely governed by the environment; that is, they must work within the confines of molecular forces such as surface tension and crystal growth processes.

Foraminifera must be examined in this new light if we are to advance in our understanding of them. Foraminifera are not molluscs; they do not have their sophisticated biological systems; we must stop looking at them as if they do.

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A CASE HISTORY IN RETROGRADE EVOLUTION: THE *ONCA* LINEAGE IN ANOLINE LIZARDS.
I. *ANOLIS ANNECTENS* NEW SPECIES, INTERMEDIATE BETWEEN THE GENERA *ANOLIS* AND *TROPIDODACTYLUS*.

Ernest E. Williams

Abstract. A new anole species bridges the gap between the genus *Anolis,* diagnosed by the presence of adhesive subdigital pads under phalanges ii and iii, and *Tropidodactylus,* diagnosed by the absence of such pads: *Anolis annectens* has typical anoline transverse lamellae with microscopic hairs and free distal margins only under phalanx ii; the third phalanx has only keeled infradigital scales as in the species *onca* currently referred to the monotypic genus *Tropidodactylus.* The genus *Tropidodactylus* is formally synonymized with *Anolis.* A morphological series in the reduction of the anoline adhesive pad that culminates in the condition seen in the species *A. onca* is described.

The genus *Tropidodactylus* was erected in 1885 by Boulenger in the second volume of his classic Catalogue of the Lizards in the British Museum (Natural History) to receive the single species described as *Norops onca* by O'Shaughnessy in 1875.

Neither the genus nor the species has received much attention since their description. They have, up to the present, been very poorly known. The validity of the genus has not been questioned, since the difference between *Tropidodactylus* and *Anolis* in the defining character of digital structure has seemed a sharp and important one: all *Anolis* (including all those species classically referred to *Norops*) have under phalanges ii and iii expanded adhesive digital pads, the smooth, flattened, transverse lamellae of which are provided with microscopic hairs (Ruibal and Ernst, 1965; Hiller, 1968; Maderson, 1970; Lillywhite and Maderson, 1968). The adhesive pad may be narrower or wider, may be sharply set off ("raised") from phalanx i or not so set

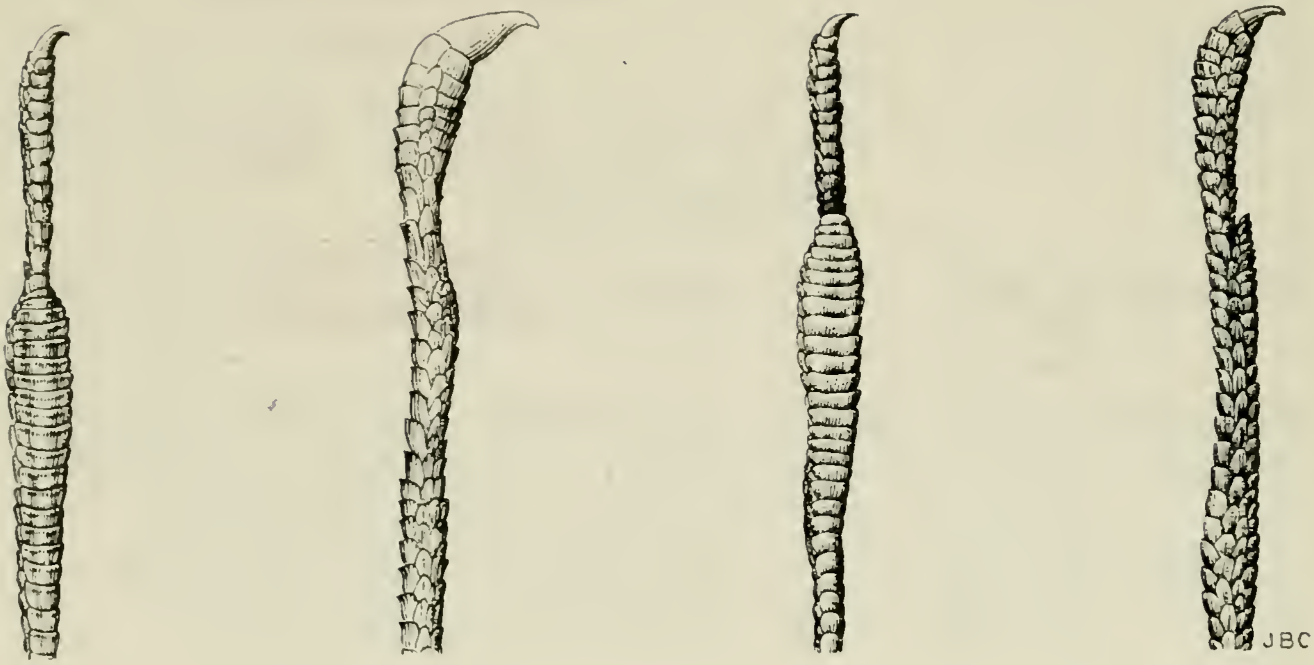

Figure 1. Left: toe of an anole showing the *"Norops"* condition; Right: toe showing the typical *Anolis* condition.

off (the *Norops* condition) (Fig. 1) and may have more or fewer lamellae, but there is always some expansion, always smooth transverse flattened lamellae under phalanges ii and iii, and always microscopic hairs. *Tropidodactylus,* as known from the single species *onca,* has been believed to differ in the complete absence of the hairs and of smooth lamellae and in the presence of multiple keels on the infradigital scales. Although in general habitus, including the presence of a large and typically anoline dewlap, the species *onca* has unmistakably the appearance of *Anolis* and is often so identified in collections; the digital difference has always been regarded as quite worthy of generic distinction. It seemed to support this position that, according to Ruthven (1922), *Tropidodactylus* seemed more terrestrial than any *Anolis:* "All of the specimens taken (17) were on the ground. It is very shy and at the slightest cause for alarm dashes into a hole."

However, Etheridge (1960) was unable to find any osteological character on which to separate *onca* generically and regarded this species as the terminal, most specialized member of his beta section of the genus *Anolis.* He was willing to retain the genus only on the basis of "the evolutionary significance of the loss of typical anole subdigital lamellae and the accompanying alteration in mode of life."

George Gorman (1969), describing the karyotype of *onca,* found it to resemble closely two of the more primitive (or "typical") members of the beta group within *Anolis* (*A. lineatopus* and *A. opalinus*). The *onca* karyotype (2n=30) with seven macrobivalents and eight microbivalents is characteristic of this group within *Anolis,* and *onca* even resembles *A. opalinus* in clear heteromorphism in chromosome pair seven. The only obvious difference found by Gorman was that pair seven appeared relatively smaller in *onca* than in the two compared Jamaican anoles, "i.e. it might be considered an intermediate between macrochromosomes and microchromosomes."

New collections of *onca* have been made by James Collins on Margarita Island (reported by him in 1971), by Carlos Rivero-Blanco and Abdem R. Lancini on the mainland of Venezuela in and near Coro, by Bryan Patterson and the members of his paleontological expedition in the same region, by the author, A. S. Rand and A. R. Kiester on the neighboring Paraguana Peninsula, and by the author, Jane Peterson, K. Miyata and R. Salvato on the Paraguana isthmus and on the east side of the Goajira Peninsula.

However, very surprisingly, as a summary of our knowledge of the species *onca* was being prepared, a unique specimen in the collection of the Field Museum of Natural History demonstrated the existence of a new species that is an ideal intermediate between the genera *Tropidodactylus* and *Anolis* as currently conceived. Differing trivially from *onca* in color and in somewhat greater size of the dorsal scales, it differs sharply in having *smooth* lamellae under phalanx ii of the fourth toe, but *keeled* scales under phalanx iii. It thus becomes impossible to make a separation of two genera in the fashion that has hitherto been customary. It is necessary either to describe a new monotypic genus for the new species or to submerge *Tropidodactylus* in the synonymy of *Anolis.* I choose the latter course and describe the new species as:

Anolis annectens new species

Holotype: FMNH 5679, adult male.

Type locality: Lago de Maracaibo, collected by W. H. Osgood between late January and early March, 1911.

Head (Fig. 2): Head stout, a little longer than tibia. Head scales unicarinate, 10 scales across snout between second canthals. A shallow frontal depression. Nasal scale separated from rostral by two intervening scales.

Supraorbital semicircles separated by one row. Supraocular

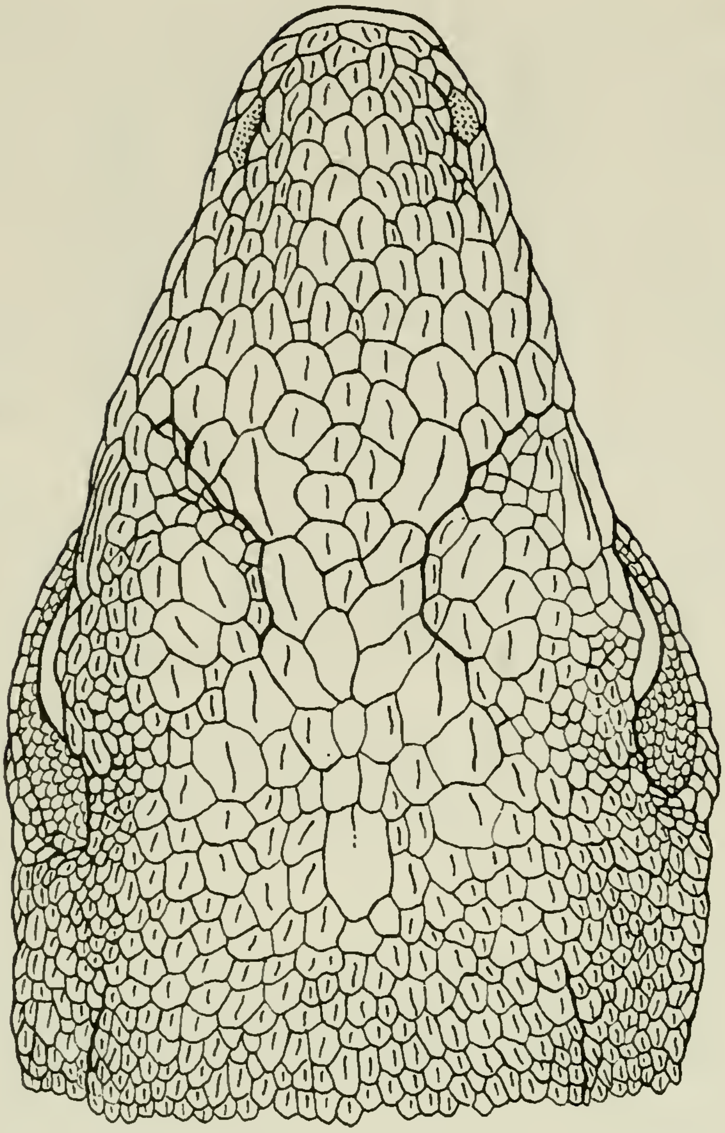

Figure 2. Head of *A. annectens* Holotype, dorsal view.

disk ill-defined, consisting of about 12 keeled scales, the largest anteromedial, the disk separated by two rows of granules from the scales of the supraciliary rows. Two parallel elongate supraciliaries continued posteriorly by a double series of moderately enlarged scales. Canthus distinct, canthal scales 5, second canthal scale largest. Loreal rows 6, the lowest row not much larger than those above it. Interparietal almost equals ear, separated from the supraorbital semicircles by 2 scales. Temporal and supraorbital scales keeled, smallest in center of temporal region, dorsally grading into larger scales surrounding interparietals. Scales behind interparietal somewhat smaller than those lateral and anterior to it.

Suboculars separated from supralabials by one row of scales, anteriorly not continued to canthal ridge, posteriorly ending abruptly with one enlarged scale. Ten supralabials to center of eye.

Mental wider than long, in contact posteriorly with 7 unicarinate scales between infralabials. No differentiated sublabials, but scales in center of throat smallest.

Trunk: Middorsal scales enlarged, hexagonal, keeled, grading laterally into much smaller but keeled flank scales. Ventrals much larger than dorsals, unicarinate, the keels in line. Postanal scales not differentiated.

Dewlap: Large, scales smaller than ventrals, keeled, arranged in widely spaced rows except at the edge.

Limbs and digits: Hand and foot scales multicarinate. No scales on limbs as large as ventrals, unicarinate. *Eight rather narrow lamellae under phalanx ii* of fourth toe, *scales under phalanx iii* of fourth toe *multicarinate.*

Tail: Tail round, all scales keeled, only ventral scales larger than dorsals, 4 scales above, 3 below.

Size: 67 mm, snout–vent length.

Color (in alcohol): Grey-brown with vague blotching and mottling on flanks, limbs and tail more distinctly barred. A round dark spot above each shoulder and a smaller spot between these on the neck middorsally. Narrow oblique transverse bands connect the shoulder spots across the middle of the back. A transverse band directly in front of shoulder, indistinct on the right side. On posterior midline two black spots, one in front of sacrum, and one between two lateral sacral spots. Dewlap scales are white, with black pigment around the bases of some of them.

Comparison with onca. Scales: The variation in squamation seen in *onca* O'Shaughnessy completely includes that of the single specimen of *annectens* except in two regards: the greater size of the dorsal scales in *annectens* (Fig. 3) and the presence under phalanx ii of smooth lamellae (Fig. 4).

Color: The color of *annectens* may also differ from that of *onca* but the variability of *onca* is so great that the rudimentary pattern seen in the type of *A. annectens* seems easily derivable from an *onca* pattern. Nevertheless there is no exact or nearly exact match in any of the extensive series of *onca.* The shoulder spots of *onca* are roughly triangular or elongate, not round, as in *annectens.* The neck spot and the two posterior midline spots of *annectens* are not exactly matched in *onca.* The peculiar distribution of dark pigment on the dewlap skin in *annectens* is again without real parallel in *onca.*

Color in life of *annectens* is unknown. However, it may be presumed from its similarity to *onca* that at least in body pattern the preserved animal gives a very fair impression of the live ani-

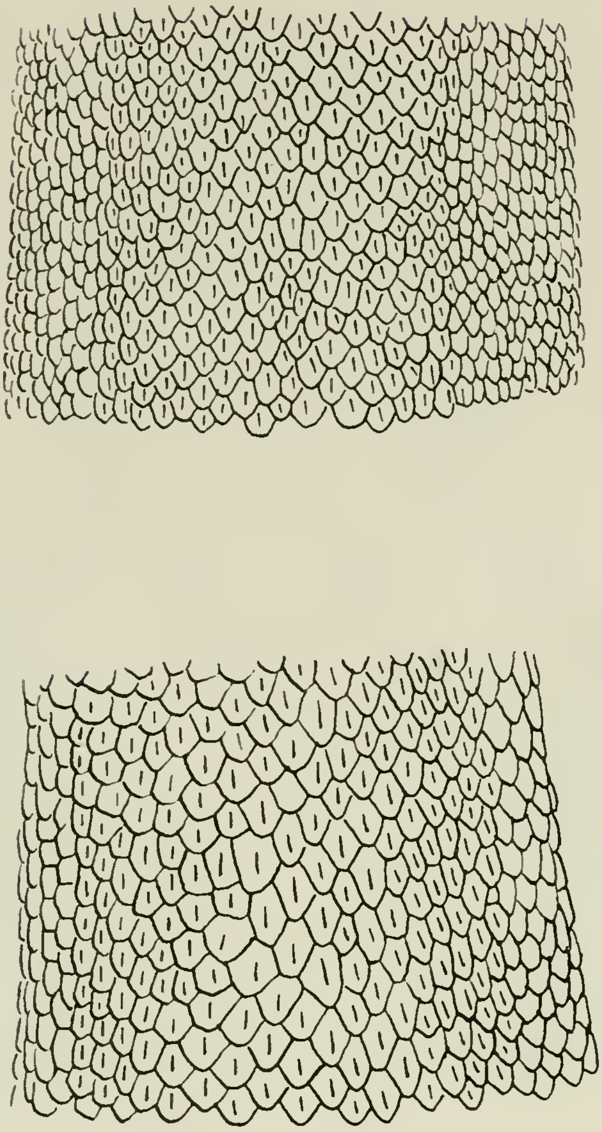

Figure 3. Dorsal scales. Above: *A. onca.* Below: *A. annectens* Holotype.

mal. Dewlap color, however, cannot safely be inferred from specimens long preserved and this might be important.

A good description of color in life by William E. Duellman of *onca* from 3 km SW of Cumana in Sucre, Venezuela, follows: "Dorsum light brown mottled with gray, gray brown and black. Venter creamy white, lightly flecked with grayish brown. Tail medium brown above, cream below. Dorsolateral mottling on WED 28685 forms more or less distinct paravertebral blotches which are gray centrally and outlined in black. Dewlap bright greenish ochre centrally, becoming orange peripherally, the whole dewlap reticulated with bright orange brown and bearing white scales. Iris bronze. Lining of throat bluish gray." [WED field notes.]

Distribution: The locality for *A. annectens* is, most unfortunately, inexact. It is not known whether Osgood collected the

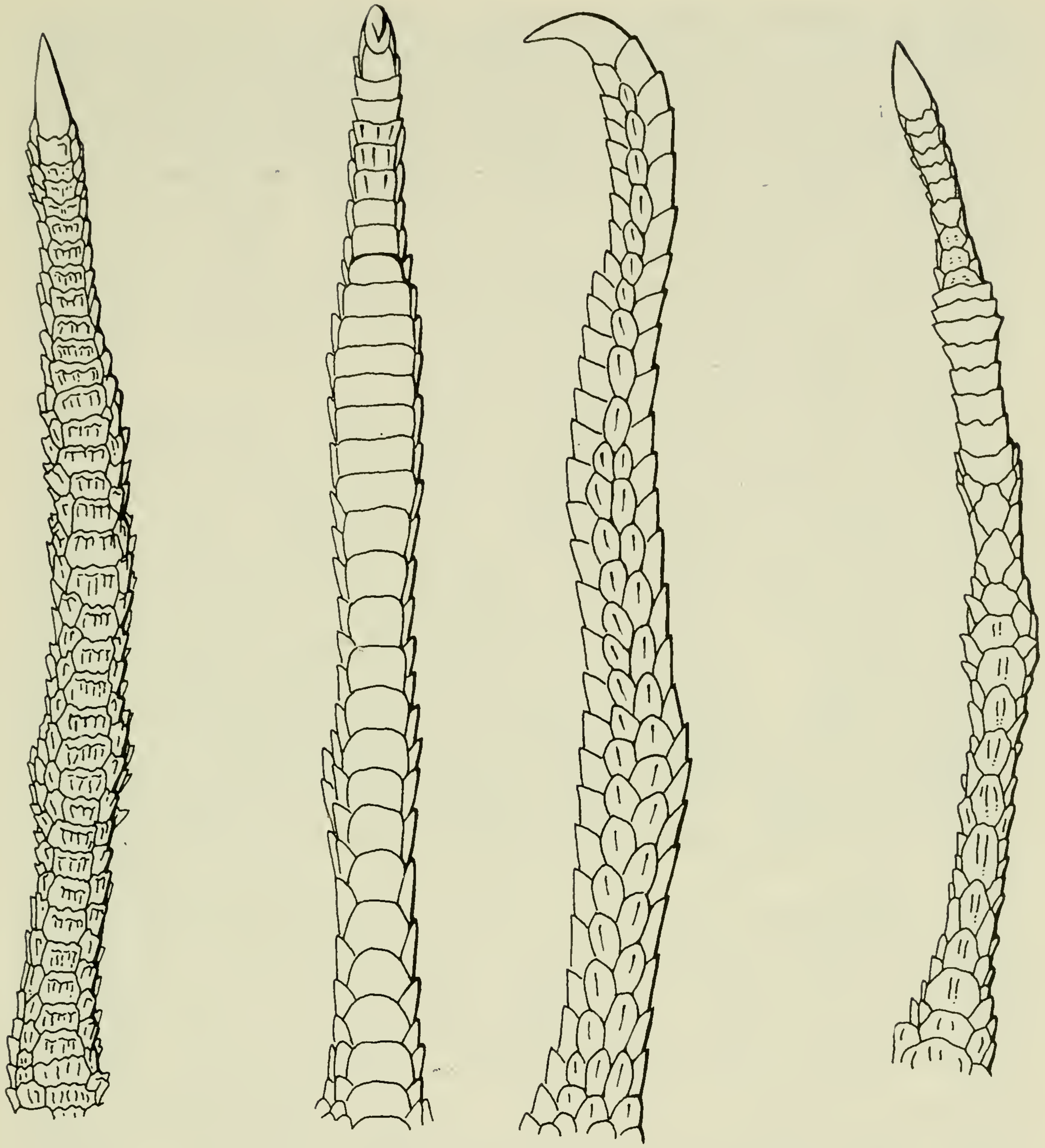

Figure 4. Fourth toe lamellae. Left: *A. onca.* Right: *A. annectens* Holotype. In the center the 4th toe of *Anolis* ("Norops") *auratus* is shown in ventral and lateral view for comparison.

specimen himself or had it brought to him, but the very inexactitude of the data and the absence of any further field notes for the specimen (H. Marx, personal communication) indicate most probably that Osgood did not have personal knowledge of the collecting site. One additional specimen — an *Anolis auratus* (formerly *Norops auratus*) — in the Field Museum received from Osgood has the same inexact data. *A. auratus* is an animal occurring in open grassy lowlands and, less abundantly, in barren thorn scrub with much cactus. It is a natural first hypothesis that *A. annectens* has a similar ecology.

Osgood (1912) reports the itinerary of his 1911 expedition to western Venezuela and eastern Colombia rather fully. Only two of his stations are plausible for *A. annectens* in terms of the expectation of a lowland grassy or arid habitat: El Panorama 8 miles due east of Maracaibo and the Empalado Savannas 30 miles further east. It is more probable, however, that both *A. annectens* and *A. auratus* were among "the few specimens from other places . . . obtained from natives in Maracaibo." However, an effort to discover *annectens* by collecting in a variety of habitats on both sides of the Lago de Maracaibo in November 1972 and August 1973 was unsuccessful. For the present no better localization of this extraordinary annectant species is possible.

The distribution of *A. onca* is much better known, though some of the literature records are clearly errors of identification or of locality. The British Museum types described by O'Shaughnessy were cited as from "Venezuela" and "Dominica." The latter locality is certainly erroneous (Barbour, 1914[1]). Specimens reported by Marcuzzi (1954) and Aleman (1952, 1953) from interior Venezuela are misidentifications. I record below only the localities that I have personally verified by examination of specimens (see Fig. 5):

COLOMBIA. *Guajira.* Cabo de la Vela: FMNH 165159. Two hours E El Cabo, near Cabo de la Vela: MCZ 85441. El Cardon, S Cabo de la Vela: RNHL 7707. Maicao: USNM 115067. Manaure and Pajaro areas: USNM 151517–23. Media Luna, E Cabo de la Vela toward Bahia de la Protete: MCZ 85440. Puerto Lopez, E shore Bahia Tucacas: MCZ 81554. Rancheria del Cabo de la Vela: ZMA 14916. Riohacha: UMMZ 54799, 54801–07, 54810–13; MCZ 14637.

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[1] On Barbour's inquiry Boulenger wrote "The *Tropidodactylus onca* was purchased of a dealer (Mr. Cutler). The locality Dominica is, therefore, open to doubt."

VENEZUELA. *Distrito Federal.* Near Caracas: USNM 107321. *Falcon.* Bahia de las Piedras, Paraguana: RNHL 7708 (3). Barunu, Buenavista, Paraguana: ZMA 14917. Cerro de Machuruia, E Santa Ana, Paraguana: RNHL 7709. El Mainon ca. 5 km N Urumaco: MCZ 133453. Isthmus of the Paraguana Peninsula: MCZ 133456–65. Istmo de Medanos: UCV 272, 300, 461, 488. Los Algodones, 28 km NW Coro: MCZ 112386–98. Los Chipes, 41 km W Coro: MCZ 112399–407. Medanos de Coro: ILS 743. Paraguana Peninsula: MCZ 133264–65 (hatched in Panama from females taken in Venezuela), UCV 485. Parque Los Orumos, Coro: MCZ 139349–50. Punta Baroa, Paraguana: UCV 448, 561. Rio Condore, vicinity of Urumaco: MCZ 133455. Rio Seco on Caribbean between Coro and Urumaco: MCZ 132735. Urumaco: MCZ 132734. *Monagas.* San Antonio de Maturin: MCZ 14648. *Margarita Island.* Boca del Rio: ILS 578. Between El Agua and Puerto Fermin: MCZ 109014, 110068–70. Near El Agua on road from Punta de Piedras to Porlamar: MCZ 110064. Ensenada de la Guardia, Laguna Arestinga: MCZ 110067. Guacuco: UCV 364, USNM 139072, MCZ 110057. Laguna Arestinga: ILS 102. Las Morites: ILS 1208. Las Robles: USNM 79226–27. S Las Robles, Porlamar: RNHL 7710 (3). Matasiete: ILS 584. Morro de Moreno: RNHL 7711. Porlamar: ZMA 14918 (2). Plantio oeste de la Asuncion: ZMA 14915 (2). Three kilometers west of Porlamar: MCZ 110397. Salamanca: ILS 561, 1231. *Sucre.* Cumana: KU 117080. 2.5 km SW Cumana: KU 117079. 3 km SW Cumana: KU 104369–70. *Zulia:* south of Paraquaipoa, W side Lago de Maracaibo: MCZ 139352.

Many of these localities are coastal, but although Collins believes *onca* to be a beach animal on Margarita Island, some verified continental localities are well inland (*e.g.,* Urumaco, Falcon, Venezuela). All localities, however, are extremely arid lowland, usually within the zone called in the Holdridge terms adopted by Ewel and Madriz (1968) for Venezuela "monte espinoso tropical." A few records appear to lie in an adjacent zone, "monte muy seco tropical." A few lie outside even this zone, *i.e.,* USNM 107321 "near Caracas" and MCZ 14648 "San Antonio de Martin." These, however, are very imprecise localities. Figure 5 shows the distribution of "monte espinoso tropical" and "monte muy seco tropical" for Venezuela according to Ewel and Madriz. The Colombian localities are similar.

However, the observations of the field party in the summer of 1973 suggest that the requirements of *onca* are more specific than just the zone "monte espinoso tropical." Search for additional specimens of *A. annectens* led us into zones clearly within the mapped areas but in which *onca* was apparently absent. *Anolis auratus* was taken in these areas. (See the ecological remarks below.)

Ecology

The relictual digital pad of *annectens* would seem to imply a somewhat greater arboreal adaptation than that of *onca*. But how terrestrial is *onca?*

No more recent observer supports the apparent implication of Ruthven's (1922) statement that *onca* uses burrows. On Margarita Island Collins (1971) looked particularly into this point. He remarks: "At times, a specimen being pursued would run into a large hole in the sand opening into a tunnel. It should be noted, however, that these holes are resting places made by ghost crabs (*Ocypode*) and are not dug by *Tropidodactylus*. It should also be noted that this was a rather infrequent mode of escape, used by the lizard only when almost completely exhausted." Collins points out that *onca* does climb when the vegetation permits this. Where the vegetation was only a mat of vines and branches, *onca* would clamber over or into this. However, "in the area just north of Punta Montadero where Mallotonia, a woody-stem plant, is dominant, the animal's behavior was very different. Here, when sighted, the lizard was always on the ground. When pursued, the majority of animals observed would merely run among the ground cover. A few specimens, however, were observed to climb the Mallotonia, some to a height of 30.0 cm. Their climbing was clumsy and ineffective."

Collins also took one animal sleeping on a branch of a low bush.

On the continental mainland the observations of Carlos Rivero-Blanco in July and August, 1970, are very useful. He reports nine specimens taken on trunks of planted trees in a park (Parque Los Orumos in Coro) within one meter from the ground and two more taken in the same park from low branches between one meter and a meter and a half above ground. Elsewhere, in more natural situations, he reports them from piles of dry branches and *inside* hollow dried cardon and cactus branches partly buried in sand. He reported, however, that the local

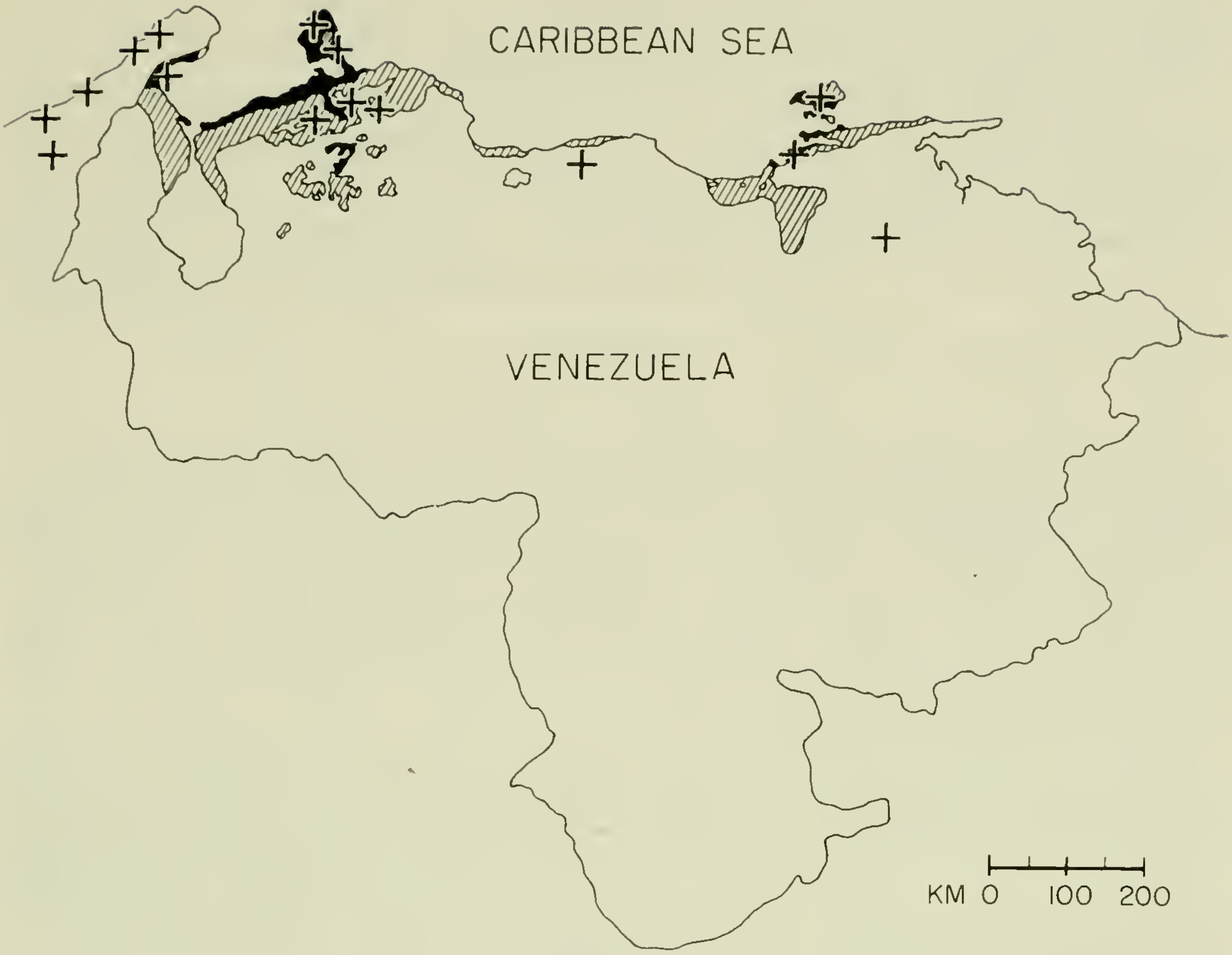

Figure 5. Map of the distribution of *A. onca.* Shading shows two vegetational zones in Venezuela (after Ewel and Madriz): black = "monte espinoso tropical;" cross-hatched = "monte muy seco tropical." + marks known localities for *onca.*

people said that *onca* could be seen on the branches of a local spineless euphorbiacean.

One of the animals obtained by the Patterson party in July to August, 1972, had been taken on the outside wall of the doctor's house in Urumaco. Again, most specimens observed were among the branches of piles of dead plants buried in sand (at Rio Seco, one to a pile). In another area one specimen was seen lying motionless on a cobble in the full sunlight. Another in still another area was seen on open ground in full sunlight, very cryptically colored and detected only by its motion.

The November 1972 party found males widely spaced out on top of the pipe line that runs much of the length of the Isthmus of the Paraguana Peninsula. Some were displaying. Others had climbed to the top of posts, including fence posts. The remainder, taken by day, including all females and the one juvenile, were on the ground in bare open spaces. None were seen in vegetation. Only one individual — a female — was taken at night, sleeping on a low bush less than a foot above the ground.

The August 1973 field party found *onca* primarily inside the low thorn bushes that are very characteristic of the Paraguana Peninsula, apparently coming out of the depths of these early in the day and clambering around within these bushes much more often than outside of them. Individuals were indeed seen on the ground and both returning to and emerging from the thorn bushes, but less frequently. Males were seen on the pipe line and on fence posts but were not seen perched on rocks in open sun in August as they had been so often in November. The small thorn bushes were shared to some extent with young *Cnemidophorus lemniscatus,* which climbed skillfully within and on top of the bushes. As during the earlier visit to the Paraguana, no *onca* were seen under or on the occasional large, quite extensive thorn bushes.

The small thorn bushes of the Paraguana Peninsula provide a very dense matrix in which climbing without adhesive pads is obviously easy. The compact bases masked by grass also provide places of concealment for *onca* and very probably sleeping sites.[1]

The August 1973 party searched for *onca* and *annectens* in many areas between Coro and Maracaibo, but only located *onca* again S of Paraguaipoa on the east side of the Goajira Peninsula (= the west side of Lago de Maracaibo). This area closely matched the Paraguana Peninsula in appearance and especially in the character of the vegetation, including the sparse cover of thorn bushes of small to moderate size.

Anolis auratus was repeatedly observed in areas in which *onca* was lacking and never where *onca* occurred. It is clear that *auratus* is less stenotopic than *onca.* It has been seen in lush grassland, abundantly on a fence row beside a cattle pasture, and sparsely in bare and harsh thorn scrub, often in situations that seem climatically more rigorous than those from which *onca* is known.

Aridity is certainly not the factor determining the presence of *onca.* A special vegetational structure does seem characteristic but there is another feature that may be even more important. The notes by Rivero-Blanco call attention to the constant high wind in the areas in which he observed *onca.* The November 1972 and August 1973 field parties also found the winds an impressive feature of the Paraguana isthmus. The *onca* locality on the east side of the Goajira Peninsula was similarly windy. The Patterson group, working well inland at Urumaco, were constantly buffeted by wind also. Such winds may be a real hazard and difficulty for lizards, preventing any strongly arboreal adaptation, and wind in combination with aridity and sparse vegetation may delimit the habitat of *onca*.

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[1] Further data on the ecology, including thermal ecology, of *onca* will be presented by Kenneth Miyata.

Discussion

The majority of iguanid lizards have infradigital scales with multiple longitudinal keels. *Tropidodactylus onca* in this regard appears by "the rule of parsimony" to have retained a primitive condition. Why then do Etheridge, Gorman and myself consider *onca* the derived extreme in anoles rather than the most primitive surviving species? The hypothesis that a reversal of evolution has produced a rather perfect simulacrum of a primitive character state seems *prima facie* less plausible and more complicated than a view that accepts an apparently primitive character as genuinely so.

The argument is in fact a simple one: in no other regard does *onca* seem primitive. In every character that Etheridge's skeletal analysis regards as important, *onca* stands closest to the most derived members of the beta section of *Anolis*. Etheridge (1960: 60) comments: "Except for the absence of specialized lamellae, it is in no way distinguished from other anoles. Other features of the genus, e.g. the absence of both splenial and angular, absence of pterygoid teeth, reduction of the parasternum (= inscriptional ribs, Etheridge, 1965) etc. indicate that *"Tropidodactylus"* is a specialized rather than a primitive anole. According to Ruthven (1922), the genus is strictly terrestrial, yet all other features which mark the anoles as arboreal lizards are present. Evolutionary loss of the anoles' specialized lamellae, rather than retention of the pre-anole condition, probably offers the most reasonable explanation of the [loss of] lamellae in *Tropidodactylus*."

In karyotype also *onca* departs very much from the 12 macrochromosome-24 microchromosome pattern that occurs repeatedly in primitive anoles, other diverse groups of iguanids (and in other lizard families) and is believed to be primitive for the Sauria generally (Webster, Hall, and Williams, 1972). The primitive karyotype is found in many members of Etheridge's alpha section of *Anolis* but in no betas, and, as Gorman (1969) has noted, *onca* belongs karyotypically, as in skeletal characters, to one of the more highly derived groups of beta anoles.

Two external features are very characteristic of most *Anolis* — the throat fan or dewlap and the adhesive pad with microscopic hairs. Both are sometimes reduced within the genus (Williams, 1963). Both *onca* and *annectens,* however, have the dewlap very large and very mobile, extremely well developed. *A. onca* is known to use the dewlap very actively (observations of the field party in November 1972), flashing it repeatedly, a derived and not a primitive feature (Rand and Williams, in preparation).[1] Of the two most basic anole characters, it is only the second — the adhesive pad — that is absent in *onca* and transitional in *annectens.*

Some of the species that show the first stages of the degradation of the digital pad have been separated taxonomically as the genus *Norops.* Schmidt (1939), describing the Mexican species *A. barkeri,* called attention to the difficulty, made obvious by more than one generic assignment for several of the species, of making consistent distinctions between the genera *Anolis* and *Norops.* Schmidt himself, though he placed *barkeri* in *Anolis,* recorded the terminal phalanges of *barkeri* as "less distinctly set off from the widened portion than in the normal *Anolis.*"

Moreover, it is now clear that any definition of *Norops* based on digital features includes species that cannot be closely related. *Anolis aequatorialis* and *A. mirus* of the trans-Andean regions of Ecuador and Colombia have *Norops*-type digits but are members of the alpha subdivision of the genus (Etheridge, 1960; Williams, 1963) and hence are on the other side of a basic dichotomy within anoles from Cuban *A. ophiolepis,* Mexican *A. barkeri, A. tropidonotus,* Colombian *A. notopholis,* central Brasilian and northern Bolivian *A. meridionalis,* and northern South American and Panamanian *A. auratus,* all anoles with *Norops*-type digits (or an approach to them but belonging to Etheridge's beta subdivision).

Even within the beta subdivision the species showing the *Norops*-type condition are not closely related to one another. Figure 6 adapts Etheridge's 1960 figure of beta anole relationships to show the independent origin of the species of *"Norops."* The numerals refer to the number of attached and free inscriptional ribs; both the total number and the number of attached ribs tend to decrease from primitive to advanced forms.

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[1] Dewlap "flashing" is very characteristic of the possibly related forest species, *Anolis chrysolepis.*

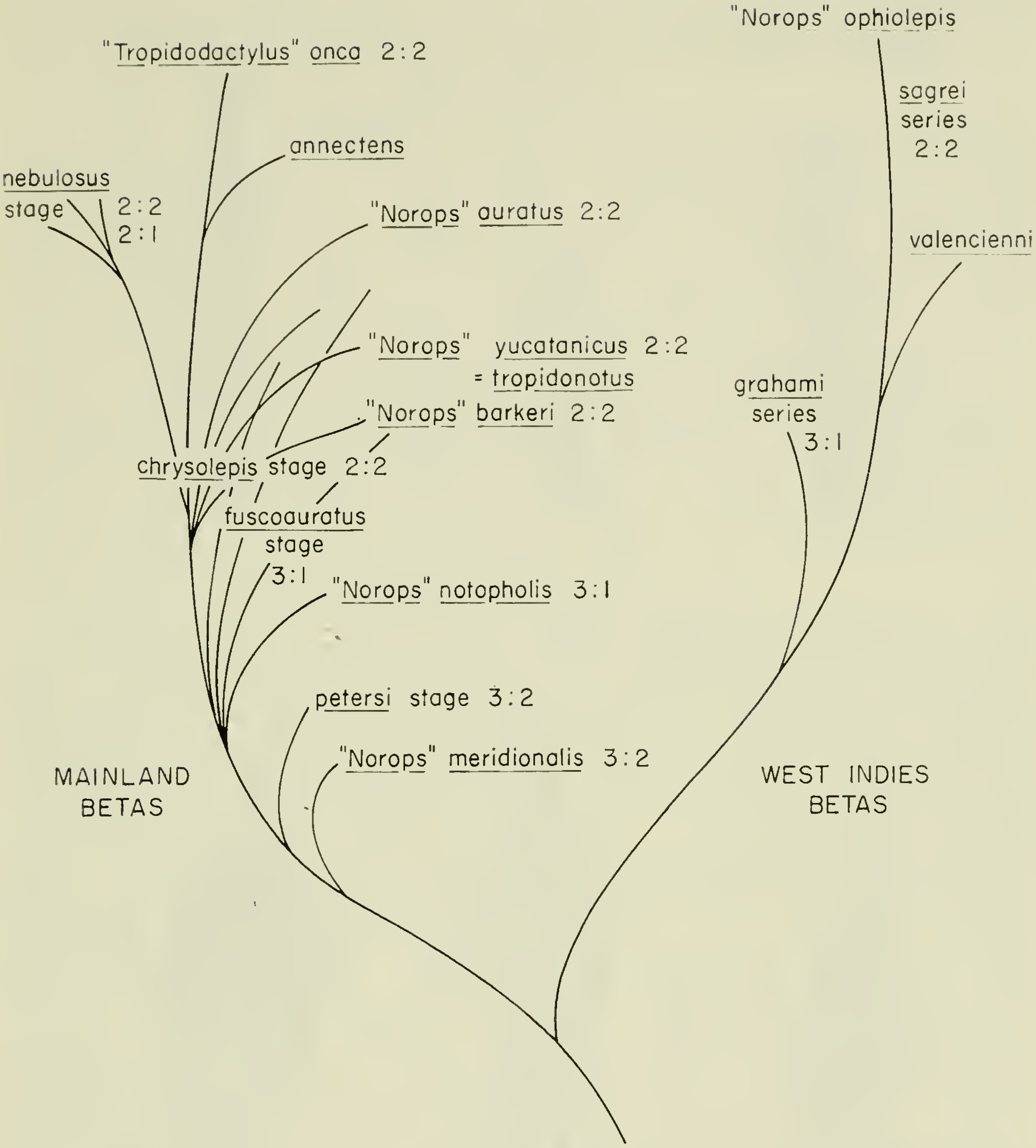
"Norops" ophiolepis
"Tropidodactylus" onca 2:2
sagrei series 2:2
annectens
nebulosus stage 2:2 2:1
"Norops" auratus 2:2
valencienni
"Norops" yucatanicus 2:2 = tropidonotus
grahami series 3:1
"Norops" barkeri 2:2
chrysolepis stage 2:2
fuscoauratus stage 3:1
"Norops" notopholis 3:1
petersi stage 3:2
"Norops" meridionalis 3:2
MAINLAND BETAS
WEST INDIES BETAS

Figure 6. A dendrogram of relationship within the beta anoles. Modified from Etheridge (1960).

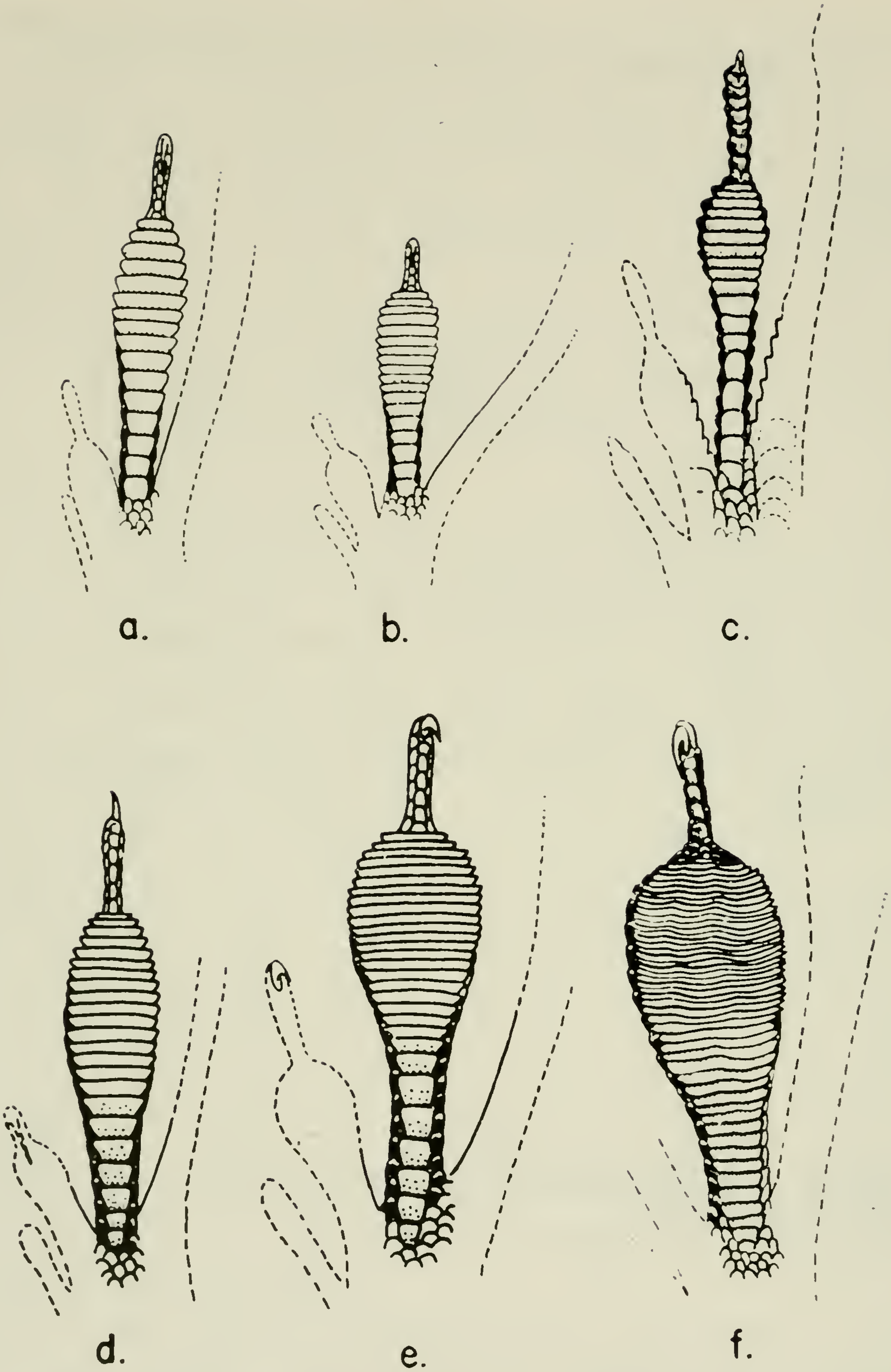

Figure 7. (from Collette, 1961). Feet of five Cuban and one mainland species of *Anolis* showing lamellae on the third toe of the left hind foot: (a) *alutaceus,* (b) *angusticeps,* (c) *sagrei,* (d) *carolinensis,* (e) *porcatus,* (f) *equestris.* Not to scale.

Phylogeny apart, *Anolis* species can be arranged in a sequence showing clear morphological stages in retrograde evolution.

1. *Narrowing of the digital dilations.*

Within any local *Anolis* fauna of more than a few species, there are several conditions of the adhesive pads which Collette (1961) has related to "arboreality." The broadest digital pads are found in those species — "crown," "trunk-crown" and "twig" anoles of Rand and Williams (1969) — which live high in the trees or use twigs and leaves as perches (*e.g., A. porcatus* and *A. equestris* in Figure 7e, f [copied from Collette, 1961]). There is also some correlation with size, but those species specializing on the lower trunks and the ground — "trunk-ground" anoles of Rand and Williams (1969) — have strikingly narrowed pads although they may be larger than some of the compared species (*e.g., A. sagrei* in Fig. 7c).

2. *Reduction of the number of digital lamellae.*

While there is an evident functional difference between a wide and a narrow pad in terms of area of adhesive surface, it is not functionally obvious what the number of transverse smooth "lamellae" has to do with adhesion, especially since many of the lamellae in those species with the highest numbers are far distal, crowded, small and much narrowed (*i.e.,* at the tapering distal end of the pad). It is, however, an empirical generalization (and not only for *Anolis;* cf. Hecht, 1952 for the gecko *Aristelliger*) that the number of lamellae has a positive correlation with size and with climbing efficiency. Correspondingly, those anole species which climb least and use the ground more show fewer lamellae than species of the same size with more arboreal habits. Again contrast *A. sagrei* in Figure 6 with *A. porcatus.*

3. *Loss of distinctness of the anterior margin of the pad* (*that part under phalanx ii*) *as against the scales under phalanx i.*

This is the character — the loss of "raised" character of the pad — that has classically defined *Norops* (*e.g.,* Boulenger) (see Fig. 3 center: *"Norops" auratus*) and is the maximal degree of dedifferentiation of the pad seen except in *annectens* and *onca.*

The functional meaning of this stage is again unclear. But it should be pointed out again that the phenomenon is not anoline only and that genera have classically been recognized in the Gekkonidae on whether the claw arises at the end of the adhesive pad or "within the pad," *i.e.,* dorsal to it, in the latter case providing the pad with a projecting lip just as in Schmidt's "normal *Anolis.*"

4. The fourth and next to final stage in this retrograde series

is found in *annectens.* As an intermediate between *"Norops"* and *Tropidodactylus* it is interesting and perhaps unexpected. In *annectens* the scales under phalanx iii are no longer either wide or smooth; they are instead narrow and keeled. Under phalanx ii, however, there is a residual pad, very narrow, it is true, and the lamellae few in number, but still recognizably a remnant of the classic anoline pad. The area under phalanx ii is in any anole the region of the pad's maximum width (and presumed effectiveness). One must assume that there is still some selective value to the presence of a minimal adhesive pad in *annectens.* However, the partial reversion to keeling in *annectens* and the total reversion in *onca* may, perhaps, be more easily understood in terms of morphogenetic patterns than in terms of direct function in the environment: supradigital scales are usually keeled in *Anolis;* unkeeled scales there are exceptional. The modified scales underneath the digit — the adhesive pad — are obviously a specialized and limited morphogenetic field. The distinctness and perfection of this field must be maintained by a continuing functional need greater than the cost in ontogenetic complexity of maintaining the specialized field. A reversion to the keeled condition of the infra-digital scales, first under phalanx iii and then also under phalanx ii, may therefore be no more than the spread of the morphogenetic field of the supradigital scales around and under the digit once the utility — *i.e.,* the selective value — of and hence the need for local differentiation of very specialized adhesive lamellae has diminished.

5. The culmination of the retrograde series in *onca* is in one regard imperfect. Hatchling *onca* have what appear macroscopically to be lamellae under phalanges ii and iii, *not* keeled scales. First discovered in the collection of the Leiden Museum, the only preserved collection to have any very small specimens, it is now confirmed on hatchlings from eggs laid by captive female *onca* in Panama.

The "lamellae" of *onca* hatchlings are astonishing enough to require histological study. How closely do these lamellae match the lamellae of "normal" *Anolis?* Hatchlings and near hatchlings 27–30 mm in snout–vent length show "lamellae"; juveniles just a few millimeters larger (34 mm, 41 mm) already show keeled infradigital scales. How is this sharp ontogenetic change accomplished?

A proper study of this question would be a digression here. The problem has been referred to P.F.A. Maderson and he will be reporting on it. Some of his preliminary observations are, however, germane at this time. The "lamellae" of hatchling *onca* are pseudo-lamellae without the "hairs" (spinules) of the true lamellae of an *Anolis* adhesive pad. They also lack the spikes characteristic of larger juveniles (almost equal 34 mm snout–vent length) and of adults of *onca*. In contrast *annectens* has under phalanx ii anoline hairs and the lamellae have the free distal edge that is characteristically anoline.

Hatchling *onca,* thus, though they seem superficially very different, are on their way to the adult *onca* infradigital condition. The lamellar field, to return to that interpretation of the embryological basis of these several conditions, is already extremely weakened at the time of hatching and soon thereafter is wholly substituted for by the field that produces spikes and keeling.

We have here emphasized a morphological series. The *onca* hatchling is in this regard an intermediate in the series but a very different intermediate from adult *annectens.* The *onca* hatchling already shows a breakdown of the lamellae and adhesive pad and in the adult the breakdown is total. *Annectens* is on another pathway. The pad under phalanx iii — always in *Anolis* the least significant portion of the total adaptation — has in *annectens* gone completely; retrograde evolution is for this area complete. But under phalanx ii the pad is only narrowed and the lamellae reduced in number; the latter are still fully pilose, presumably still fully adhesive. A habitat for *annectens* more genuinely "arboreal" than that of *onca* does seem plausible.

Acknowledgments

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SOUTH AMERICAN *ANOLIS*: THREE NEW SPECIES RELATED TO *ANOLIS NIGROLINEATUS* AND *A. DISSIMILIS*

ERNEST E. WILLIAMS

ABSTRACT. Three new *Anolis* species are described from widely scattered localities in Colombia and Venezuela. Together with *Anolis nigrolineatus* and *Anolis dissimilis* they appear to represent a natural subgroup of the *punctatus* group of South American alpha anoles.

The lizard fauna of South America is poorly understood but more than that it is little known. It is, for example, very probable that there are many lizard species to be discovered in the continent's remoter and more obscure areas. The three new anoles here described are cases in point: they are from areas quite remote or obscure — one from a small river valley in Santander and the poorly known states of Tachira and Trujillo in Venezuela, another from a camp in remote Caqueta in Colombia, and still another from a mission in the delta at the mouth of the Orinoco.

More interesting, however, than the existence of new species in little explored areas is the close resemblance of these newly discovered, *perhaps* isolated anoles to species occurring at very great distances from them. The most extreme instance is the similarity of the anole from the mouth of the Orinoco to a form from Madre de Dios Province in Peru. However, the distances between the other forms that must be compared are relatively small only in the context of the immensity of South America.

Even in South America it is quite unusual to be compelled to describe related species from such small samples as are available for the three new forms (one, one and five), especially when these are spread over so wide an area with no series available for any locality. This may point to a special difficulty peculiar to small arboreal species. The fauna of open formations is usually obtainable in some appreciable numbers wherever it occurs. The species of forests are rarer or more difficult to obtain, but most probably both. Those elements of the forest fauna that occur well up in the trees or at least in thick vegetation are likely to be the last to be known. On morphology and affinity, although only for one is anything known directly of the ecology, the present three new species appear to belong to this most difficult group.

All three anoles are so close to *Anolis nigrolineatus* and *Anolis dissimilis* (Williams, 1965) that they, like these, must be assigned to the *punctatus* group of the alpha section of South American anoles.

A. nigrolineatus (Williams, 1965) was described from two specimens, both with questionable localities in southeastern Ecuador. Two additional specimens have since been discovered in the collections of the University of Michigan. These not only provide the first good locality for the species (Playas de Montalvo, Prov. Los Rios, Ecuador) but provide a better comparison with the new but very closely related species from eastern Colombia and western Venezuela which I call:

Anolis nigropunctatus new species

Holotype: ILS 21, an adult male.

Type locality: El Diamante, Norte de Santander, Colombia.

Paratypes (all adult females). ILS 20: Toledo, Norte de Santander, Colombia; MCNC 5395, Villa Paez, Edo Tachira, Venezuela; MCZ 136175, Quebrada Honda on road from Trujillo City to San Lazaro, Edo Trujillo, 4700 feet.

Diagnosis. Close to *A. punctatus* (cf. the slightly swollen snout in the male) but differing in color and squamation. Closer still to *A. nigrolineatus* but differing in wider head, apparently larger size (male 72 mm in snout–vent length rather than 46 mm), in the absence of the narrow middorsal black line and of the broad black spot in the dewlap. Nostril without a differentiated anterior nasal scale (Fig. 1). An apparently greater number of lamellae under phalanges ii and iii of the fourth toe (21–22 rather than 18–19).

Description. (Paratype variation in parentheses.) *Head:* Head scales flat, obscurely wrinkled. Seven scales (7–10) across snout between second canthals. Five scales (6–8) border rostral posteriorly. Circumnasal scale separated from rostral by one scale (or in contact). Four scales between supranasals. Snout

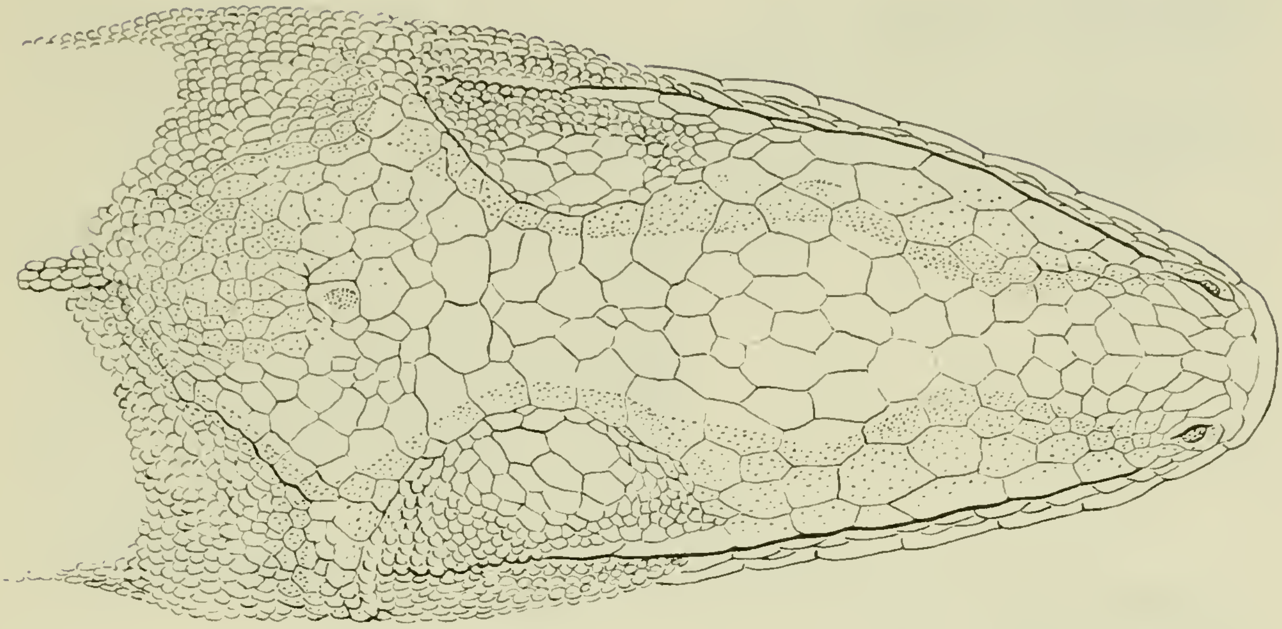

Figure 1. *Anolis nigropunctatus* Holotype. Dorsal view of head.

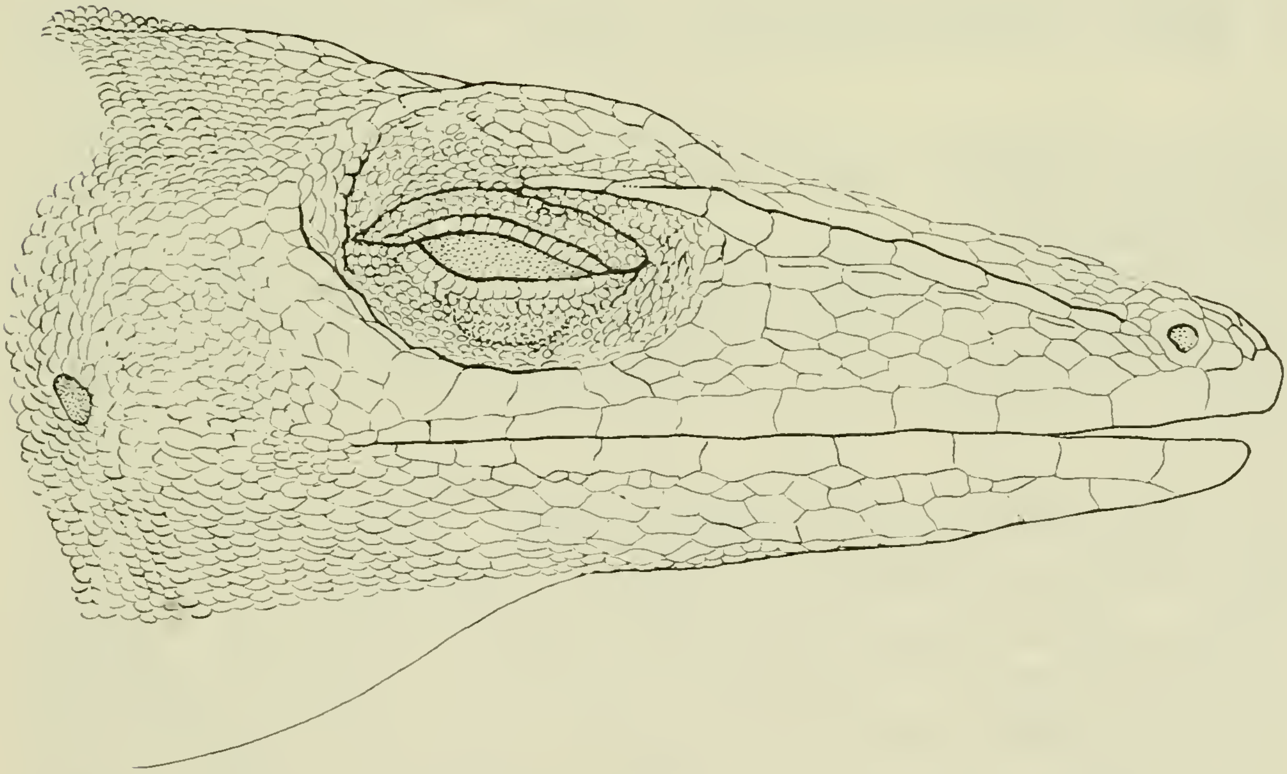

Figure 2. *Anolis nigropunctatus* Holotype. Lateral view of head.

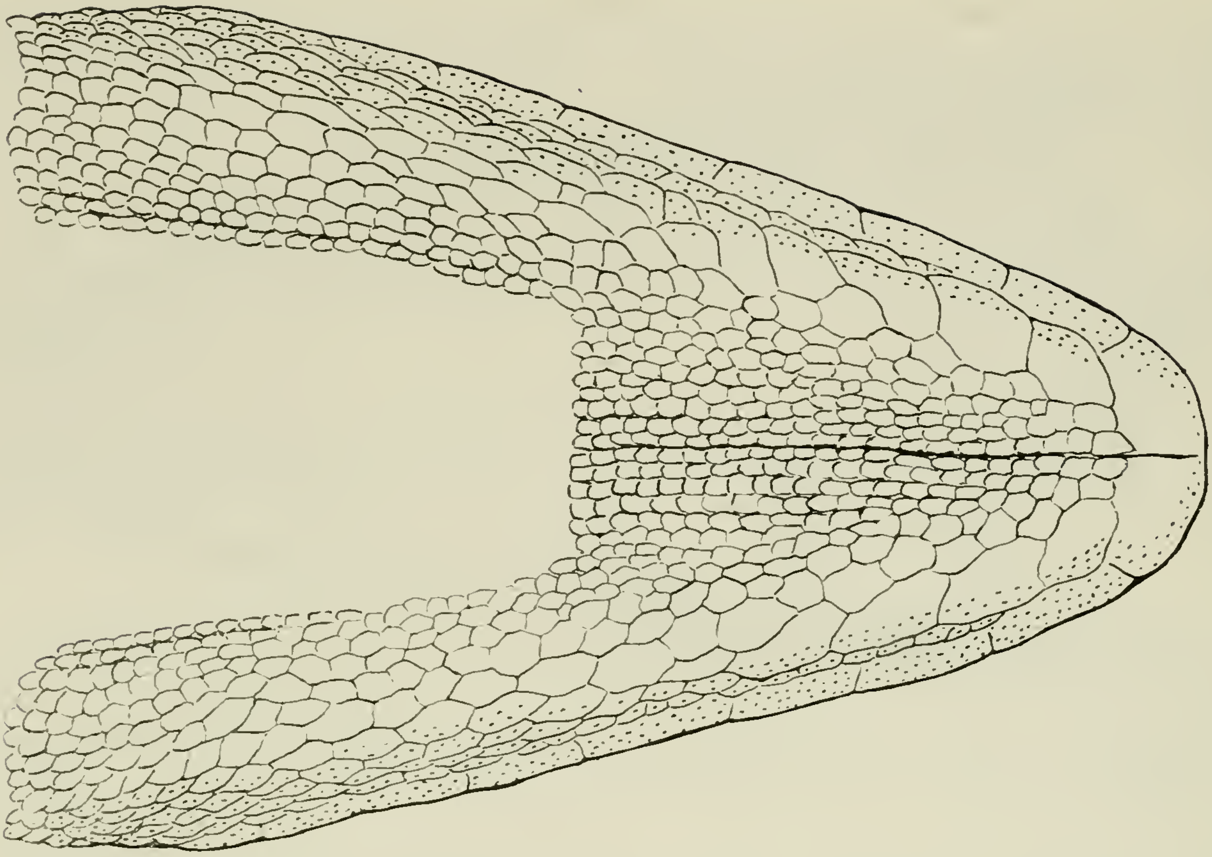

Figure 3. *Anolis nigropunctatus* Holotype. Underside of head.

somewhat swollen, protuberant, overhanging lower lip (snout not swollen in ♀).

Supraorbital semicircles separated medially by 2 scales (2 or 1 or in contact) and from the supraocular disks of each side by a single row of subgranular scales. Supraocular disk of 9 (8–12) indistinctly wrinkled scales. Supraciliaries 1–2, continued posteriorly by granules. Canthus distinct, canthals 5 (5–6), second and third canthals longest (third longest). Loreal rows 5 (4–5), uppermost largest (uppermost largest or subequal).

Temporals and supratemporals granular, grading into enlarged scales surrounding interparietal (obscure in second female), which is smaller than the small round ear (almost equals ear) and separated from the supraorbital semicircles by three (1–4) scales. Several of the scales surrounding interparietal larger than that scale (or 2/3 that size). Scales posterior to interparietal grading gradually into dorsal granules. No enlarged supratemporal rows (indistinct supratemporal rows).

Suboculars weakly keeled, in contact with supralabials, grading posteriorly into the supratemporal granules and anteriorly separated from canthals by one scale. Seven supralabials to center of eye.

Mental semidivided, each part almost as wide as deep (wider than deep), the whole in contact with 3 (4) throat scales between large, smooth sublabials which indent it. Sublabials enlarged, two (3) in contact with infralabials. Gular scales smallest medially, grading laterally toward sublabials.

Trunk: Middorsal scales not differentiated from flank scales (two middorsal rows slightly enlarged), obtusely keeled. Ventrals larger, smooth, quadrate, imbricate, in transverse rows (not imbricate). Lateral chest scales obtusely keeled (smooth).

Dewlap: Large (smaller in ♀, extending only between forelimbs), extending nearly to middle of belly. Scales at the edge much longer than ventrals (in ♀ smaller than or equal to ventrals). Lateral scales narrow, elongate, in well-spaced rows (close packed in ♀), separated by naked skin.

Limbs and digits: Scales on limbs smooth or unicarinate, largest on both arm and hind limb (smaller than ventrals). Supradigital scales multicarinate. Twenty-one (22) scales under phalanges ii and iii of fourth toe.

Tail: Compressed, without verticils or dorsal crest. Two distinctly keeled middorsal rows; the ventralmost two rows even more distinctly keeled. Greatly enlarged postanals (absent in ♀) present. Scales behind vent smooth.

Color (as preserved): ♂ above brown, irregularly punctate with black; below light brown with a few small lateral black spots. Dewlap, both scales and skin, light. ♀ same as above except with a broad middorsal zone light brown, mottled and lined with grey and dewlap with light scales and pigmented skin.

Size: Type (snout–vent length) 72 mm. Paratypes: 60, 56, 55 mm.

Comment. A. nigropunctatus (see Table 1) is extremely close to *A. nigrolineatus* but quite adequately distinct. The two newly discovered specimens of *nigrolineatus* (UMMZ 84114–15) fully confirm the scale and color characters noted in the original description and have the same small size. In the feature of a simple single scale (nasal or circumnasal scale) surrounding the nostril, I regard *nigropunctatus* as more primitive than *nigrolineatus.* The scale called "anterior nasal" in the latter I believe to be a modification of a scale originally anterior to that surrounding the nostril, now become enlarged and triangular, overlapping the anterior margin of the primitive circumnasal scale. The higher number of toe lamellae in *nigropunctatus* accord with its larger size.

Ecological notes are available only for MCZ 136175 for which J. A. Rivero records: "On leaves three feet from the ground at edge of road near a stream."

TABLE I

	nigrolineatus	*nigropunctatus*	*caquetae*	*deltae*	*dissimilis*
	SW Ecuador	NE Colombia and W Venezuela	Amazonian Colombia	Delta of the Orinoco	SE Peru
swollen snout in male	—	+	+	—	—
scales across snout	8–9	7–10	10	8	7
nasal/rostral	anterior nasal scale in contact with rostral, sometimes inferior nasal as well	no differentiated anterior nasal; circumnasal directly in contact with rostral or one rounded scale separating circumnasal and rostral	anterior and inferior nasal scales in contact with rostral	anterior nasal in contact with rostral	circumnasal scale separated by one rounded scale from rostral
scales between supraorbital semicircles	1–2	0–2	1	0	0
loreal rows	4–7	4–6	5	4	4
interparietal/ear	>	<	>>	>>	>

TABLE I — Continued

	nigrolineatus	*nigropunctatus*	*caquetae*	*deltae*	*dissimilis*
scales between interparietal and semicircles	2-3	1-4	0	0	0
scales around interparietal/dorsals	>	(>)	=	>>	=
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	7-11	7	7	7	11
lamellae under 4th toe	18-19	21-22	22	24	17
postanals in ♂	+	+	weakly indicated	—	+
middorsal scale rows enlarged	one	two	two	one (tail crest!)	one (tail crest!)
♂ size (snout to vent in mm)	45	72	57	58	56

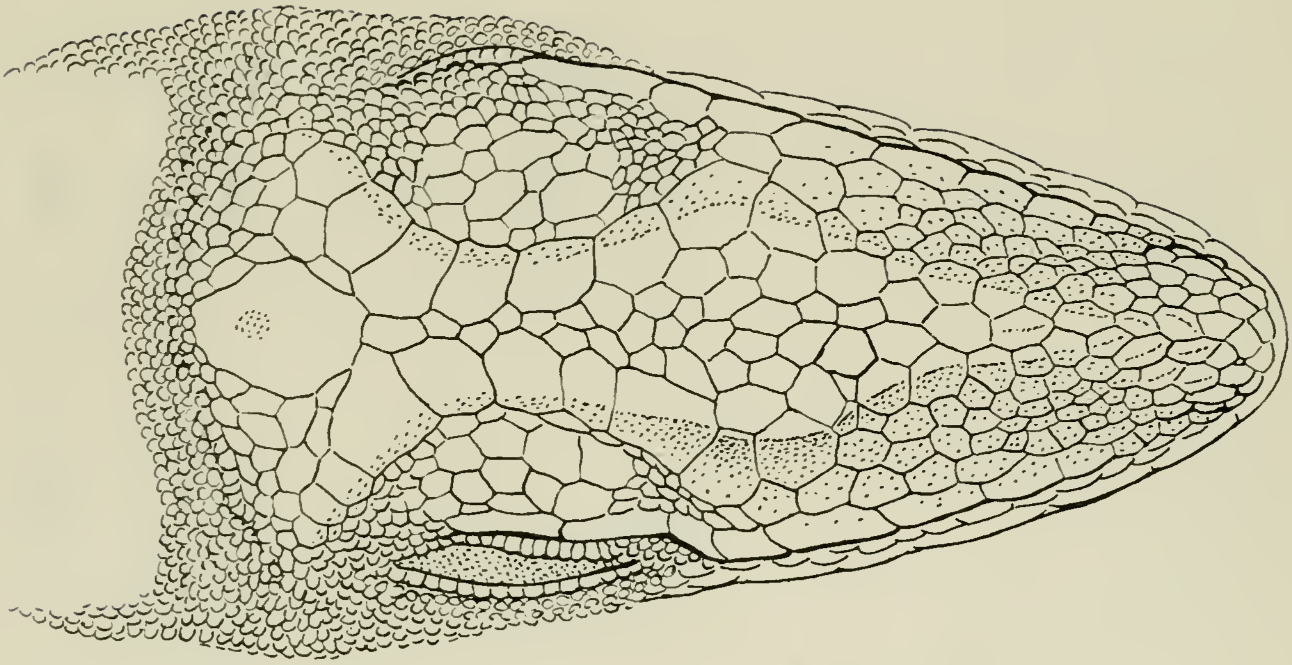

Figure 4. *Anolis caquetae* Holotype. Dorsal view of head.

The two remaining undescribed species appear to be closest to *A. dissimilis,* but the species geographically more remote is more similar than that which is spatially intermediate. The latter is clearly the primitive member of the series and, coming from the upper Rio Apaporis, is within the Amazonian faunal province but in one of the remoter peripheral parts of that region. I name it after the Department of Colombia from which it comes.

Anolis caquetae new species

Holotype: MCZ 131176, an adult male.

Type locality: Camp Soratama, Upper Apaporis, Caqueta, Colombia.

Diagnosis. Close to *A. dissimilis* but without the tail crest characteristic of that species and with a different coloration.

Description. Head: Most head scales smooth, some on the anterior snout unicarinate. Scales in frontal depression distinctly smaller than surrounding scales. Ten flat scales across snout between the second canthals. Eight swollen scales bordering rostral posteriorly. Nasal scale anterior to canthal ridge with one lower and one anterior scale separating it from rostral (see Fig. 5). Seven swollen scales between supranasals. Snout somewhat swollen, protuberant, overhanging lower lip.

Supraorbital semicircles separated from each other by a single row of small scales, in contact with the supraocular disks, which consist of 24–28 enlarged smooth scales grading into granules

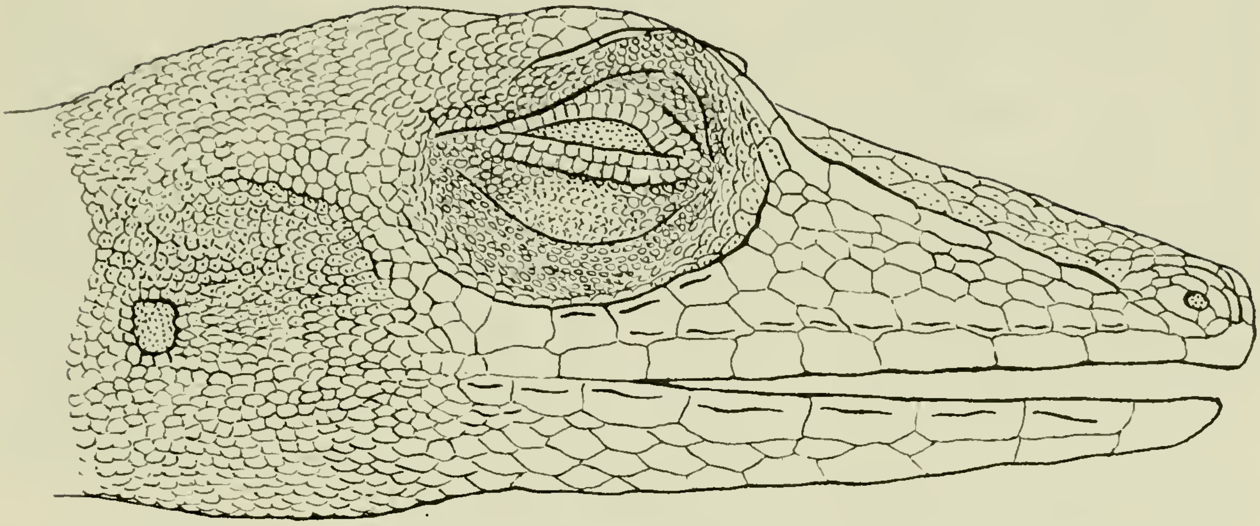

Figure 5. *Anolis caquetae* Holotype. Lateral view of head.

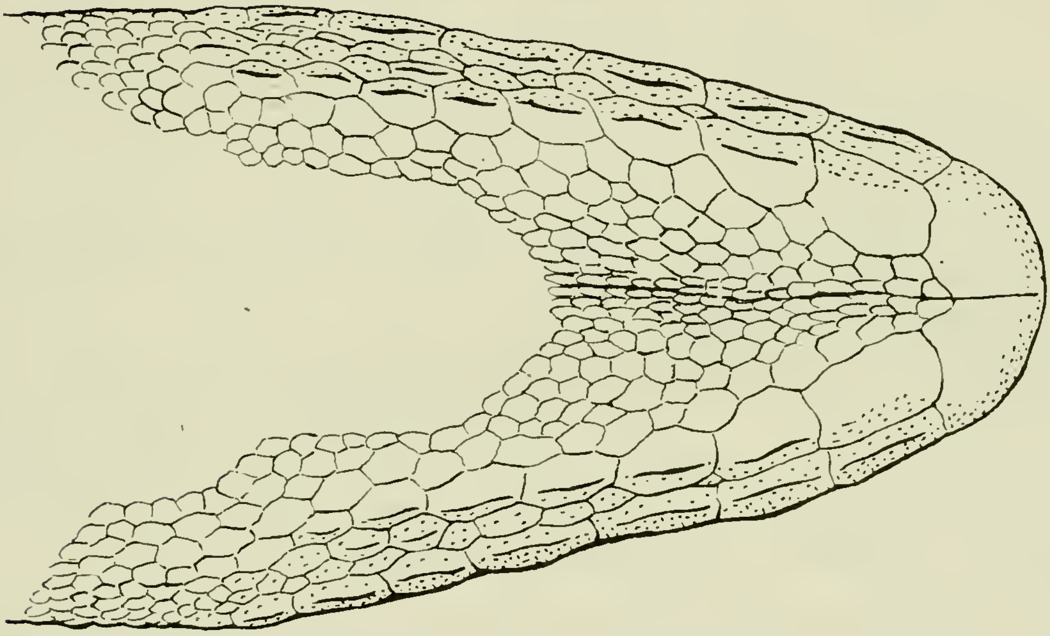

Figure 6. *Anolis caquetae* Holotype. Underside of head.

anteriorly, posteriorly and laterally. A single enlarged supraciliary continued posteriorly by granules. Canthus distinct, canthal scales 7, the third canthal largest, then diminishing gradually forward. Loreal rows 5, the lowest distinctly the largest. Temporal and supratemporal scales granular, grading into enlarged scales lateral to the interparietal. A weakly indicated double supratemporal row of large granules extending posteriorly from the orbit. Interparietal very large, much larger than the small round ear opening, in contact with the supraorbital semicircles. Scales lateral to the interparietal distinctly enlarged, but those posterior to it hardly larger than the dorsal granules, about equal to the supratemporal and temporal granules.

Suboculars smooth, broadly in contact with supralabials, grading into large granules behind the eye; anteriorly grading into loreals. Seven supralabials to the center of the eye.

Mentals deeper than wide, in contact with 4 throat scales between the sublabials. Sublabials large, wide, three to four in contact with infralabials. Central throat scales small, not grading into sublabials, swollen, vaguely keeled.

Trunk: Middorsal scales granular, swollen, smooth, not differentiated from flank scales. Ventrals larger than dorsals, weakly keeled, imbricate.

Dewlap: Dewlap small, scales larger than ventrals, close set.

Limbs and digits: Hand and foot scales obscurely multicarinate. Largest arm and leg scales unicarinate, those of the arm somewhat larger than ventrals. Twenty-two lamellae under phalanges ii and iii of fourth toe. Postanals?

Tail: Tail compressed with two middorsal rows obtusely keeled and the two midventral rows larger, sharply keeled. Verticils not evident. Lateral caudal scales increasing in size toward ventrals.

Color (as preserved): Dorsum brown with a narrow black vertebral line bifurcating on nape. Broad oblique transverse banding of obscure dark blotches, limbs obscurely banded. Belly and throat light brown, sparsely punctate with darker. Tail very obscurely banded.

Size (snout–vent length): 57 mm.

Comment. Like a number of South American anoles that do not seem closely related (*e.g., A. jacare, A. nigropunctatus*), *A. caquetae* has a double row of scales surmounting the tail rather than the more usual one. This is very different from the tail crest of a single row of enlarged triangular scales characteristic of *A. dissimilis.* This difference does not seem, however, a bar to the close relationship. A similar if less extreme difference exists between *A. nigropunctatus* and *A. nigrolineatus.* In other details of squamation *A. caquetae* and *A. dissimilis* are very much alike (Table 1). They differ strikingly, however, in color and pattern. The dark dorsal color of *dissimilis* with the light line from supralabials to shoulder has no elements of similarity to the middorsal dark line and broken crossbanding of *A. caquetae.* On the other hand, the vestigial dark line may indicate relationship to *A. nigrolineatus,* which in squamation (Table 1) differs most prominently in features associated with the huge size of the interparietal in *A. caquetae.*

The last species requiring description comes from the delta of the Orinoco. I have therefore named it:

Anolis deltae new species

Holotype: (MCN) 2031, adult male.

Type locality: Mission Araquaimujo, Delta Amacuro, Territorio Federal, Venezuela.

Diagnosis. Very close to *A. dissimilis* including the presence of a distinctive tail crest, but with a blunter, shorter head, a differentiated anterior nasal scale, a larger interparietal with larger scales surrounding the interparietal and more lamellae under phalanges ii and iii of fourth toe.

Description. Head: Most head scales smooth, swollen, a few obtusely keeled. Eight scales across snout between second canthals. Six scales border rostral posteriorly. Anterior nasal scale in contact with rostral. Four scales between supranasals. Scales in frontal depression smaller than surrounding scales.

Supraorbital semicircles in contact, separated from the supraocular disks on each side by one row of scales. Supraocular disks of 12–14 strongly enlarged scales. Supraciliaries one on each side, continued by granules. Canthus distinct. Canthal scales 6, the second and third largest. Loreal rows 4, the lowermost largest.

Temporals and supratemporals subgranular, grading into enlarged scales surrounding interparietal. Interparietal very large, larger than ear, in contact with supraorbital semicircles. Scales behind interparietal grading gradually into dorsal granules. Suboculars in contact with supralabials, grading posteriorly into supratemporal granules, anteriorly separated from the canthals by one to two scales. Seven supralabials to the center of the eye.

Mental wider than deep, in contact with four throat scales,

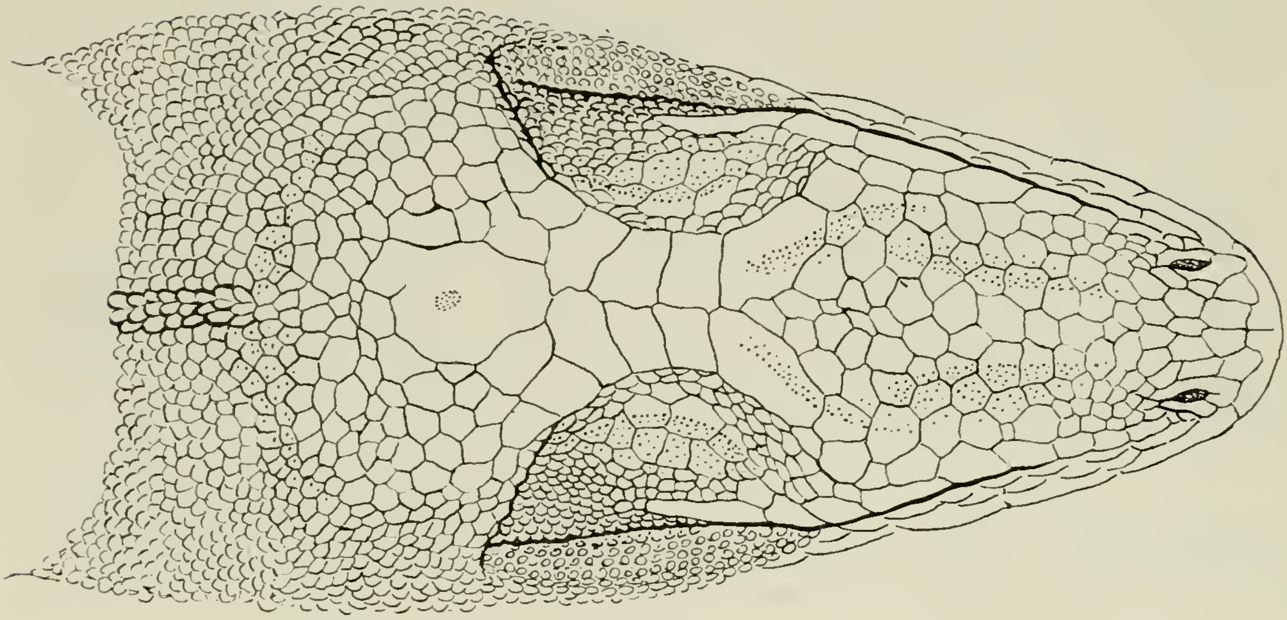

Figure 7. *Anolis deltae* Holotype. Dorsal view of head.

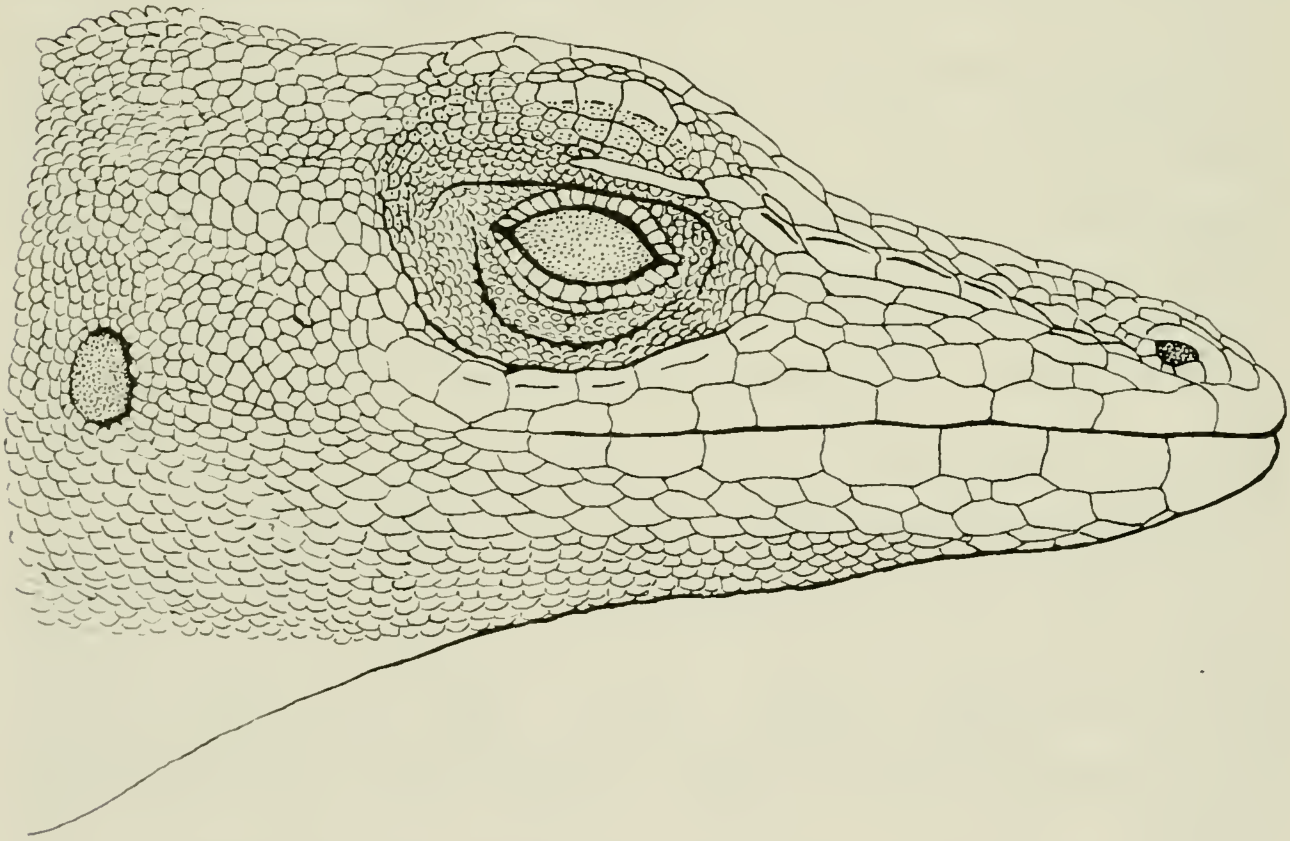

Figure 8. *Anolis deltae* Holotype. Lateral view of head.

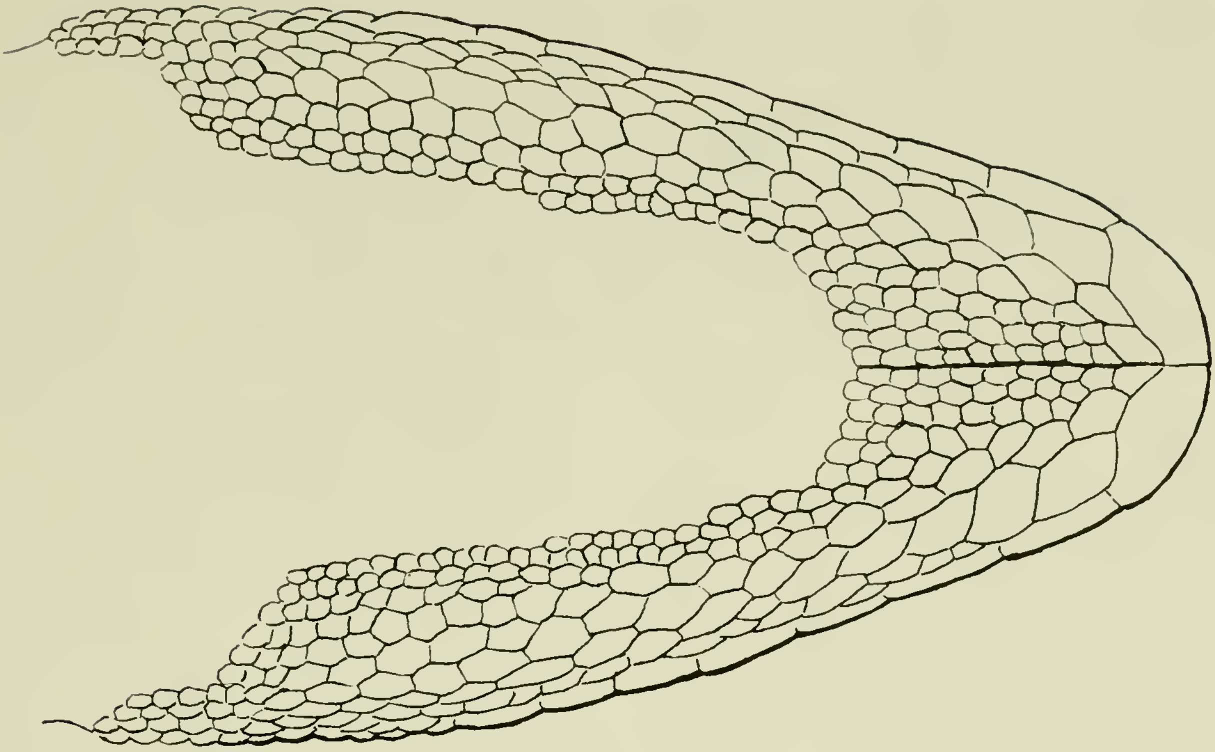

Figure 9. *Anolis deltae* Holotype. Underside of head.

set in a gentle forward arc between sublabials. Sublabials enlarged, two in contact with infralabials on each side. Gular scales subequal centrally but grading laterally into sublabials.

Trunk: A few middorsal rows slightly enlarged, obtusely keeled, grading into flank granules. Ventrals larger, smooth, quadrate, imbricate, in transverse rows.

Dewlap: Large, extending nearly to midbelly. Scales at edge as large as ventrals. Lateral scales narrow, elongate, in rows separated by naked skin.

Limbs and digits: Largest limb scales unicarinate, almost equal ventrals. Supradigital scales obscurely uni- or bicarinate. Twenty-four lamellae under phalanges ii and iii of fourth toe.

Tail: Most of tail missing but a distinct crest on the portion present. Enlarged postanals absent. Scales behind vent smooth.

Color (as preserved): Straw. A series of broad but vague darker blotches middorsally. Obscurer and quite irregular spots and mottling on flanks. Belly with vague markings. Above and below head and limbs very obscurely mottled. Dewlap skin and scales light.

Size (snout–vent length): 58 mm.

Comment. The tail crest of *A. delta*e and *A. dissimilis* in particular is a highly distinctive common feature. It is entirely a crest of slightly raised keeled scales that gives the appearance of a serrate upper border to the tail, not at all like the huge tail

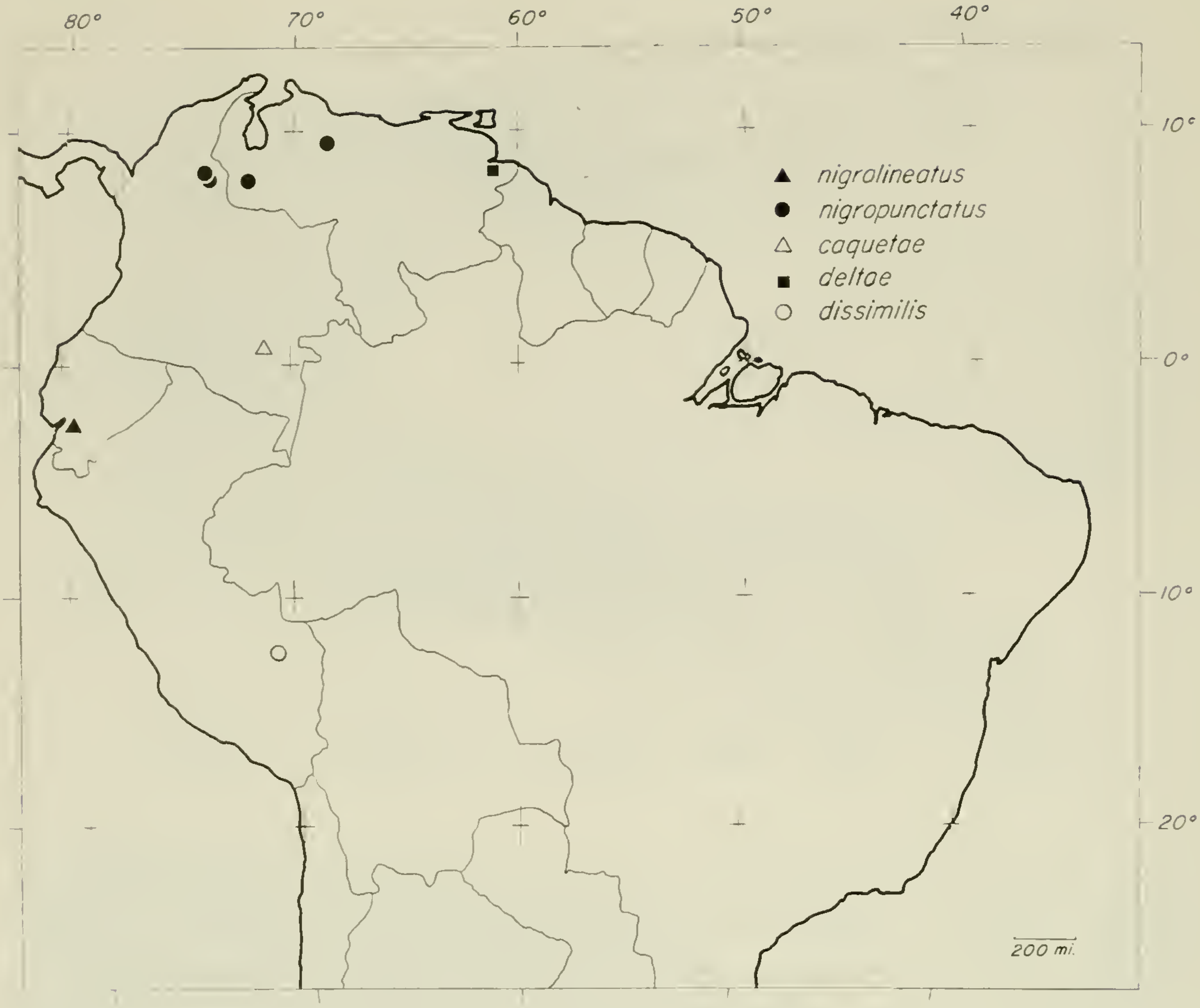

Figure 10. Distribution of the *Anolis* of the *A. nigrolineatus* subgroup.

fins supported by vertebral spines of the considerable number of West Indian species that have compressed crested tails — not therefore impressive except that it is very unusual in South America. Even the South American giants (the *latifrons* group *sensu stricto*), though they have compressed tails, lack any sort of crest. The closest resemblance in tail type is perhaps provided by the anoles of the *pentaprion* group (Myers, 1971) in which the serrate crest, however, is surely convergent, since these are beta anoles belonging to quite a distinct section within the genus *Anolis*.

A. deltae is quite different from *dissimilis* in color and pattern, closer in this to *A. caquetae* which it resembles also in the strongly enlarged interparietal. It differs, however, from both species in the enlarged scales behind the interparietal, markedly larger than the dorsals.

Discussion. The five species that have been discussed here are perhaps a natural subgroup — the *A. nigrolineatus* subgroup —

of the *punctatus* species group. They are all allopatric and they ring changes on just a few characters. If they are such a group, there are two series on the basis of affinities and geography — an inner series, peripheral to Amazonia proper, in the upper reaches of Amazonian tributaries and the Orinoco, and an outer series with one species west of the Andes in Ecuador (almost at the southern limit of *Anolis* species west of the Andes) and another in valleys in the northern and northeastern continuation of the Andes in Colombia and Venezuela.

So far as current information extends, none of these overlap with the two larger Amazonian species of the *punctatus* group — *A. punctatus* itself and *A. transversalis.* These widespread species, which show little geographic variation, lie internal to even the inner series of the *nigrolineatus* subgroup, *A. punctatus* with a very wide distribution in the Brazilian Atlantic forest, Amazonia and in the Guianas, *A. transversalis* at least partly sympatric with *punctatus* in western Amazonia. With South American anoles so little known, this apparent geographic pattern could well be factitious. However, *A. punctatus* and *A. transversalis* are among the first collected of anole species wherever they occur. Their absence from the collections that record the *dissimilis-caquetae-deltae* series may therefore be real.

Acknowledgments

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A NEW SPECIES OF PRIMITIVE *ANOLIS* (SAURIA· IGUANIDAE) FROM THE SIERRA DE BAORUCO, HISPANIOLA

ALBERT SCHWARTZ[1]

ABSTRACT. A new species of primitive anole is described from the Sierra de Baoruco in the República Dominicana. The species is compared with its relatives *occultus* (Puerto Rico) and *darlingtoni* and *insolitus* (Hispaniola). Data on the ecology of the new species, in relation to *A. insolitus* and *A. occultus,* are presented.

On the Antillean islands of Puerto Rico and Hispaniola occurs a small group of anoles which has been known from only three species, two of which were only very recently discovered and named. The earliest discovery of a member of this trio of lizards was that of *Anolis darlingtoni* Cochran, of which the holotype and still only known specimen was taken by P. J. Darlington in 1934 at Roche Croix on the northern slopes of the Haitian Massif de la Hotte on the Tiburon Peninsula at an elevation of about 5000 feet (1525 meters). Cochran (1935) named this species *Xiphocercus darlingtoni* in recognition of its resemblances to *X. valencienni* Duméril and Bibron from Jamaica. The genus *Xiphocercus* is now in the synonymy of *Anolis;* the two species are very similar in general habitus and habits but are not closely related. Etheridge (1960: 92) stated that although these two species were externally similar, they differed in critical osteological details (caudal vertebrae, number of attached and floating chevrons, and presence of autonomic septa). *X. valencienni* was like other Jamaican anoles in osteological characteristics and *X. darlingtoni* like several Haitian species. It seemed obvious that these two species were erroneously associated at the generic

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level, and that they represented a convergence between representatives of two anoline stocks of Jamaica and Hispaniola.

The second member of this complex of anoles was discovered on Puerto Rico in 1963 by Juan A. Rivero in the Cordillera Central near Cerro de Punta at an elevation of 1338 meters. *Anolis occultus* was described by Williams and Rivero (1965) from a suite of specimens from various upland Puerto Rican localities and at the same time Thomas (1965) summarized the ecological data and field observations that he had accumulated while collecting the majority of the type-series. Later, Webster (1969) presented further information on the ecology of this forest-dwelling species.

The third member of the trio was first secured by Clayton E. Ray and Robert R. Allen in 1963 at La Palma, La Vega Province, República Dominicana, at an elevation of 3500 feet (1068 meters) in the Dominican Cordillera Central. *Anolis insolitus* was described by Williams and Rand (1969) from six specimens taken at the type-locality. These authors also made extensive comparisons between *darlingtoni, occultus,* and *insolitus,* which form a small complex of primitive anoles. That they are distinct species is unquestioned. But Williams and Rand (1969: 10) noted that "Certainly the most plausible assumption based on current evidence is that *darlingtoni* and *insolitus* are geographic representatives . . . of one stock. This assumption, however, leaves the extreme size disparity of these allopatric species without easy explanation." At the time this statement was written, the largest known *insolitus* had a snout–vent length of 34 mm and the holotype of *darlingtoni* has a snout–vent length of 72 mm. The allusion of Williams and Rand to these two species as "geographic representatives" is due to the fact that one (*darlingtoni*) occurs on the Hispaniolan south island whereas the other (*insolitus*) occurs on the Hispaniolan north island. These two terms have come into common usage among herpetologists who deal with Hispaniolan amphibians and reptiles, since they apply to two island masses, formerly separated, but now joined by the low-lying Cul de Sac-Valle de Neiba plain. These two islands have, to a large extent, distinctive faunas; there has naturally been some invasion and interchange of species, but this has been primarily of lowland forms. The montane faunas of these two paleoislands remain remarkably distinct today, and it is only reasonable to assume that these montane faunas, despite a common origin in many cases, have been completely discontinuous for a very long period.

Williams and Rand (1969: 10) also pointed out that of the 21 Hispaniolan species of *Anolis,* seven had been described within the last ten years; they also stated that they felt that the list of species presented in their summary was incomplete and that "the fund of new information and of new taxa is not nearly exhausted, and the need for further collection and study is abundantly clear."

Under the sponsorship of two National Science Foundation grants (G-7977 and B-023603) between 1968 and 1972, I collected in the República Dominicana; comparable collections were made by Richard Thomas in Haiti. In the former country, we were successful in securing specimens of two new species of *Anolis.* The description of one of these (Schwartz, 1973) has already been completed. Although this species, from the Cordillera Central, is a large and exceptionally handsome lizard, it does not add materially to our knowledge of the Antillean history of the genus *Anolis.* It is a species living in deciduous forest of the Central uplands at elevations above 5400 feet (1647 meters), and as far as present evidence indicates, it is an endemic Cordillera Central species of the *monticola* complex.

The second species is far more interesting and intriguing. This anole is an inhabitant of hardwood forests in the Sierra de Baoruco, the easternmost massif of the chain of three montane masses on the Hispaniolan south island. It is in the Massif de la Hotte, the westernmost of this chain of three ranges, that *A. darlingtoni* occurs. Thus, we now know of two species of this group of anoles from the Hispaniolan south island. The doubts expressed by Williams and Rand concerning the geographical equivalence of *darlingtoni* and *insolitus* have been shown to have a sound basis, since there is little question that this new species is the south island analogue of the north island *insolitus,* and that the larger *darlingtoni* stands alone among other members of the group as a much larger lizard. Details of the relationships between all four species will be presented by Williams and Etheridge in a separate publication; it is my aim herein to describe the new species, give details of its variation, and compare it with the three remaining species, as well as to present field observations made during 1971.

The first specimen of this new taxon was observed by myself on the night of 29 August 1971, as it slept on a dry hanging vine under a low vine canopy shelter adjacent to the road in the Sierra de Baoruco. Its sleeping posture and general configuration, despite the fact that it was some ten feet (3.1 meters) above me, attested that it was a species related to *A. insolitus* and *A. occultus*. Because of the peculiar situation where the lizard slept, I was reluctant to make the attempt to secure it. This reluctance was due to the fact that I and my companions have spent many nights and days collecting in the Sierra de Baoruco since 1963 without seeing a lizard of this sort. Bruce R. Sheplan was invited to make the attempt at retrieving the lizard, and he very carefully ascended the muddy road cut, crawled gingerly beneath the vine canopy without disturbing the vegetation, and handily secured the lizard. We later learned that there was no need for such care in dealing with this *Anolis,* since, like *insolitus* and *occultus,* it is extremely tolerant of any sort of nocturnal disturbance and determinedly clings to its perch despite disturbances. A second specimen was secured later the same evening from a similar sleeping situation only 15 feet (4.6 meters) from the first individual. Two more visits to the same general area yielded a total of 16 lizards; it is obvious that at least locally this new species is not rare, but on the other hand its ecological requirements (and these can be deduced only from its sleeping sites) may be extremely rigid. The locality itself is not difficult of access and to my eye is little different from many other regions in the Sierra de Baoruco uplands, areas such as the Las Auyamas-Valle de Polo region which have been extensively collected. Still, the new species is known only from one fairly circumscribed area. In honor of Mr. Sheplan, whose care and interest not only were responsible for the first two specimens but also for most of the subsequent material, I propose that the new species be named

Anolis sheplani new species

Holotype. National Museum of Natural History (USNM) 194015, an adult male, from 13.0 mi. (20.8 km) SE Cabral, 3200 feet (976 meters), Barahona Province, República Dominicana, taken by Bruce R. Sheplan on 29 August 1971. Original number Albert Schwartz Field Series (ASFS) V30309.

Paratypes. ASFS V30310, same data as holotype; Carnegie Museum (CM) 52300, same locality as holotype, 30 August 1971, D. C. Fowler; ASFS V30326, USNM 194016–17, CM 54140–41, American Museum of Natural History (AMNH) 108822, Museum of Comparative Zoology (MCZ) 125641–42, 12.3 mi. (19.7 km) SE Cabral, 3300 feet (1007 meters), Barahona Province, República Dominicana, 30 August 1971, D. C. Fowler, A. Schwartz, B. R. Sheplan; MCZ 125691, ASFS

V30824–26, 12.3 mi. (19.7 km) SE Cabral, 3300 feet (1007 meters), Barahona Province, República Dominicana, 9 September 1971, A. Schwartz, B. R. Sheplan.

Diagnosis. A species of the *darlingtoni-occultus-insolitus* group of anoles, distinguished from all other species by the combination of: 1) small size (males to 41 mm, females to 40 mm snout–vent length) and strong lateral compression; 2) modally 2 rows of loreal scales (modally 3 or 4 in other species); 3) supraorbital semicircles modally separated by 1 row of scales (3 rows in *occultus,* 1 row in *darlingtoni* and *insolitus*); 4) supraocular semicircles separated from interparietal scale by 1 scale on each side (4 scales in *occultus,* 1 scale in *darlingtoni* and *insolitus*); 5) modally 1 enlarged scale in supraorbital disk (no enlarged scales in *occultus,* 2 in *insolitus,* 5 in *darlingtoni*); 6) rostral scale in contact posteriorly with 5 small scales (9 scales in *occultus,* 5 scales in *insolitus,* 6 scales in *darlingtoni*); 7) 4 distinct canthal scales (10 indistinct small canthal scales in *occultus,* 4 distinct canthals in *insolitus,* 5 in *darlingtoni*); 8) supralabials to center of eye 8 (10 in *occultus,* 7 in *insolitus,* 7 or 8 in *darlingtoni*); 9) 4–6 scales (mode 5) between second canthal scales (9–14 in *occultus,* 2–6 in *insolitus* with a mode of 4, 5 in *darlingtoni*); 10) a distinct supraciliary row of scales but no scale enlarged (no differentiated supraciliaries in *occultus*); 11) no postorbital, supratemporal, or occipital spines (present in *insolitus*); 12) no distinct supratemporal line of enlarged scales (present and the series enlarged and terminating in a spine in *insolitus*); 13) interparietal scale ovoid, much larger than external auditory meatus (equal in *occultus*); 14) canthal ridge strong (weak in *occultus*); 15) middorsal scales small, smooth, subequal, with a longitudinal series of isolated spine-like scales separated by about 6 to 8 small flat scales, no specialized spine-like scales on neck (no modified middorsal scales in *occultus;* nape scales slightly smaller than middorsals and no specialized spine-like scales in *darlingtoni;* nape scales forming a low nuchal crest as far posteriorly as about insertion of forelimbs, followed by low rounded and isolated bosses, composed of about 8 small rounded scales, the bosses separated by about 5 or 6 small dorsal scales in *insolitus*); 16) ventral scales smooth and distinctly larger than dorsal scales (about equal in *darlingtoni*), juxtaposed, in often poorly defined transverse rows; 17) dewlap large, slotted (= inset), in both sexes, pale peach in males, brown with a cream border in females (pinkish gray in both sexes of *occultus;* rich mustard, brown, orange or orange-ocher in both sexes of *insolitus;* color unknown and dewlap not slotted in *darlingtoni*); 18) limb scales smooth, those on anterior face of thigh as large as ventrals (smaller than ventrals in *occultus,* weakly carinate in *darlingtoni*); 19) supradigital scales smooth (multicarinate in *darlingtoni*); 20) tail round with a continuation of the evenly spaced middorsal spines, dorsal caudal scales larger than ventrals, smooth to weakly unicarinate, ventral caudal scales much larger, strongly unicarinate (no dorsal caudal scale modification in *occultus,* dorsal scales very small, granular, ventral caudal scales larger, smooth, and smaller than ventrals; dorsal caudal scales modified into a series of irregularly spaced large triangular scales in *insolitus,* dorsal and ventral caudal scales unicarinate and ventral caudals larger than ventral scales); 21) a pair of enlarged postanal scales in males (none in *occultus*); 22) general coloration very pale (almost white) but capable of pale tan to dark brown phases, or lichenate blotching of these two colors with a row of tiny dark brown dots down middorsal line, these dots the enlarged median dorsal spinose scales; a small black to dark brown nuchal dot and a broad dark sacral U in the pale phase; two black radiating lines from the eye onto the temporal region and a ventral radiating line from the eye which, ventrally, forms one of a maximum series of five incomplete transverse dark brown to black lines crossing the throat, the most posterior at the anterior end of the slotted dewlap; venter white.

Description of holotype. An adult male with the following measurements and scale counts: snout–vent length 40 mm, tail length 43 mm; 4 canthal scales; 5 snout scales at level of second canthal scales; 3 vertical rows of loreals; supraorbital semicircles separated by 1 row of scales; 1 scale on each side between the interparietal and the supraorbital semicircles; subocular scales and supralabial scales in contact; 1 large scale in the supraocular disk; 2 postmental scales; 6 small scales in contact with the rostral scale posteriorly; 8 supralabials to center of eye; 14 subdigital lamellae on phalanges II and III of fourth toe. Coloration of holotype. When collected at night, very pale tan (almost white), but capable of limited metachrosis to pale tan at one extreme and dark brown at the other; often assuming a lichenate blotched pattern of pale tan and dark brown, with a row of tiny dark brown dots down the dorsal midline, these dots corresponding to the individual enlarged and spaced spinose middorsal scales; in the pale phase, a black to dark brown nuchal dot and a dark broad sacral U; tail banded red-brown and tan, the red-brown bands narrow, five in number including the tail tip, and separated by tan interband areas that are twice the width of the dark bands; a pair of fine black lines radiating onto the temples from the eye on each side, and a fine black line extending ventrally from the eye across the supralabials onto the throat where it forms the central of five incomplete dark crossbands across the throat, the most posterior of which is at the angle of the jaws; dewlap large, slotted, very pale peach, venter very pale tan laterally, white centrally.

Variation. The series of *A. sheplani* consists of 16 specimens of which one (MCZ 125691) has been skeletonized and upon which no external counts or measurements were taken. Of the remaining 15 lizards, nine are males and six are females. The largest male has a snout–vent length of 41 mm (MCZ 125641) and the largest female 40 mm (ASFS V30310). Both sexes thus seem to reach about the same adult size; males are easily distinguished at any age by the presence of a pair of enlarged postanal scales. The series includes four young lizards with snout–vent lengths between 20 mm and 25 mm. The canthal scales are large and clearly delimited and always 4. There are between 4 and 6 scales across the snout at the level of the second canthals (mode 5). The loreal rows are either 2 or 3 (mode 2). The supraocular semicircles are either in contact or separated by 1 or 2 rows of scales (mode 1). The scales between the interparietal and the supraocular semicircles are almost always 1 bilaterally, although two specimens have 2 scales in this position unilaterally. The subocular scales are always in contact with the supralabial scales, of which there are between 7 and 10 (mode 8) to the center of the eye. There is modally only 1 enlarged scale in the supraorbital disk, but three lizards have 2 scales (the second enlarged but much smaller than its companion) in the disk. The postmental scales vary between 2 and 5 (mode 4) and there are 4 to 8 small scales (mode 5) in posterior contact with the rostral scale. In further discussion of scutellar characters, I follow the schema established by Williams and Rand (1969) for this group of anoles.

Head: Narrow, elongate. Head scales large, smooth, smallest anteriorly. Nostril circular, nasal scale separated from rostral by 3 small oval scales. Rostral scale wide, low, in contact with 4 to 8 small scales posteriorly.

Supraorbital semicircles large, weakly convex, the scales slightly boss-like, either in contact or separated by 1 or 2 rows of smaller scales. A much less distinct row of many small oval scales along the supraciliary margin on each side, no elongate

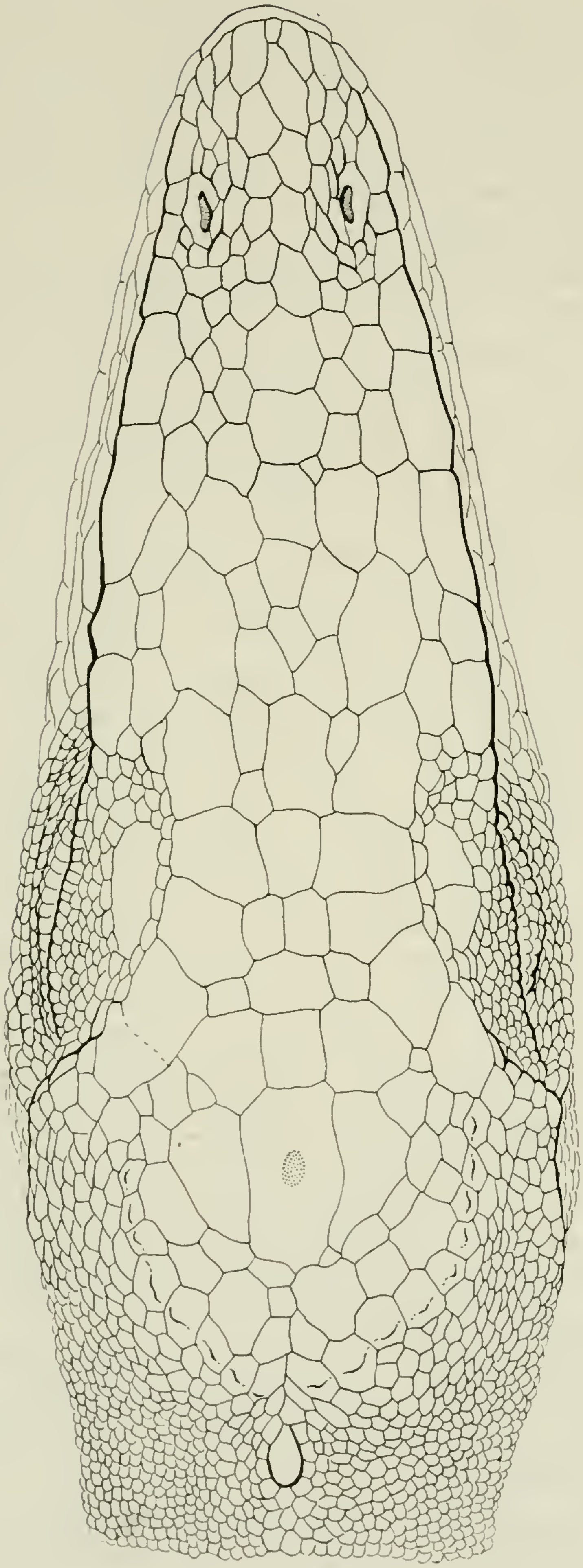

Figure 1. *Anolis sheplani* Holotype. Dorsal view of head. Illustrations funded by NSF grant GB-37731X to Ernest E. Williams.

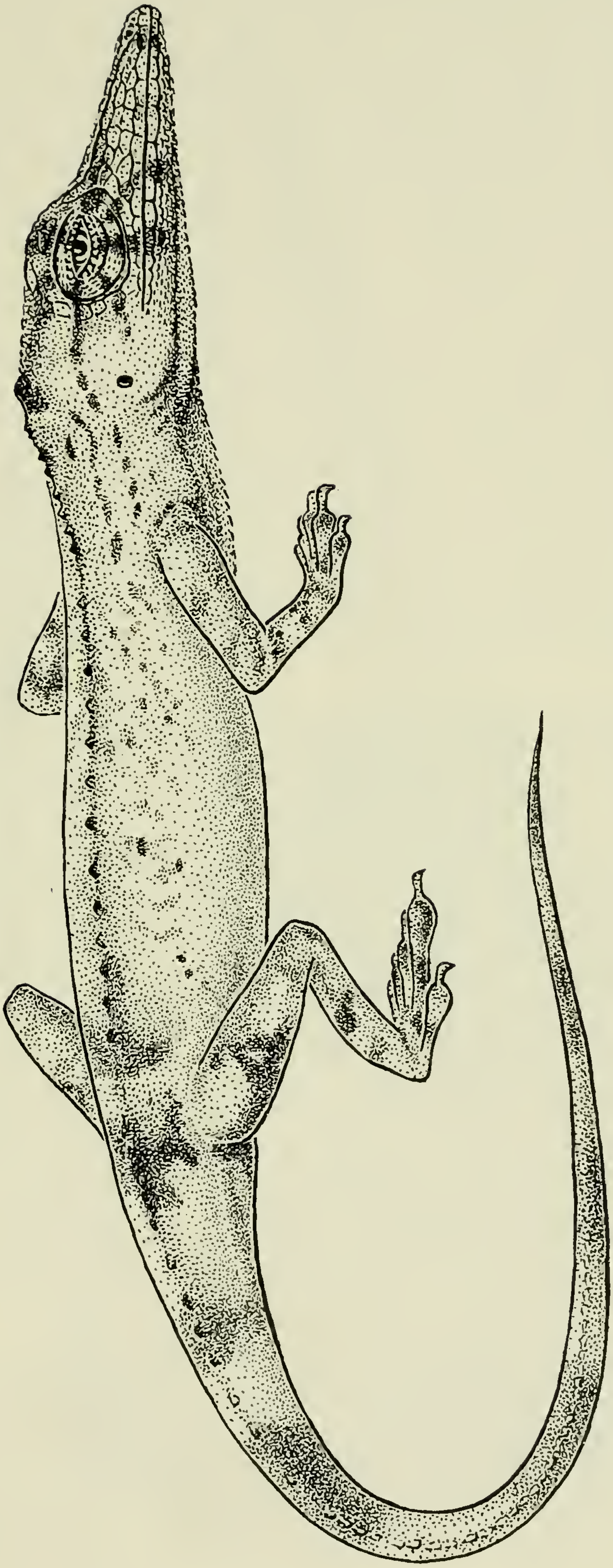

Figure 2. *Anolis sheplani* Holotype. Lateral view of head.

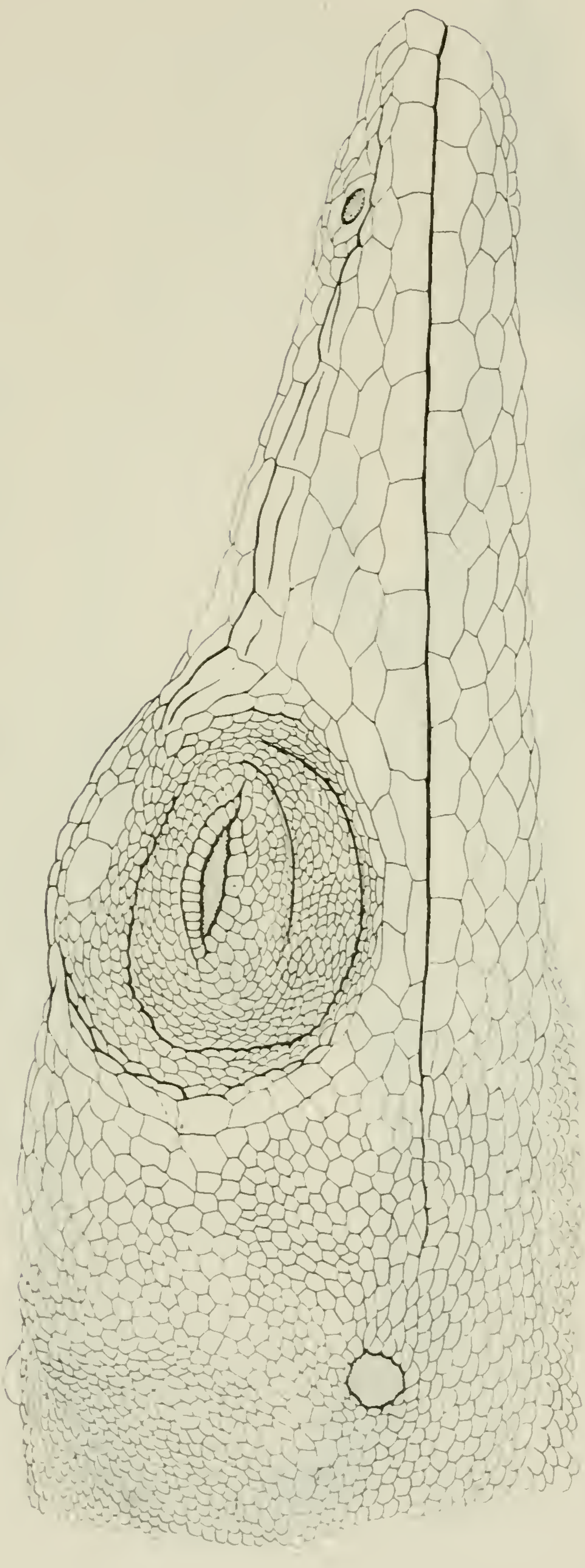

Figure 3. *Anolis sheplani* Holotype. Lateral view.

supraciliary scale. Posterior and interior to the supraciliary row, 3 or 4 rows of small scales or granules of which the most interior are largest, surrounding the single (occasionally two) enlarged scale in the supraorbital disk. Canthal ridge of 4 scales well defined, second canthal longest, diminishing in size anteriorly, anteriormost posterior to nostril and separated from it by the posterior portion of the nasal scale. Loreal rows 2 or 3, the scales varying in shape between elongate rectangular and quadrangular. No distinct supratemporal line or row of scales. Temporal scales small, flat, about 14 between the enlarged postocular scales and the external auditory meatus. Supratemporal scales flat and gradually larger than temporals, not forming a U-shaped crest behind the interparietal region. Interparietal ovoid, very much larger than tiny external auditory meatus, separated on each side usually by 1 (occasionally 2) scale from the supraocular semicircles. Scales surrounding interparietal flat, without prominent tubercles or spines. External auditory meatus very tiny, elliptical, placed far ventrally, just dorsal to the comissure of the mouth.

Suboculars directly in contact with supralabials, anteriorly grading into loreals, posteriorly continuous with the enlarged postoculars. Seven to 10 supralabials to center of eye.

Mental large, semidivided, wider than deep, in contact with 2 to 5 small granular postmental scales; 1 infralabial and 1 sublabial in contact with mental on each side. Throat scales smooth, elongate anteriorly, becoming more granular and ovoid posteriorly, gradually merging with the ventral scales.

Trunk: Dorsal scales small, smooth, slightly larger on flanks, and merging with the ventral scales; a middorsal series of individual spinose crest scales, separated by about 6 to 8 unmodified dorsal scales, this middorsal series of spinose scales continued onto the dorsal caudal midline. Ventrals larger than dorsals, smooth, rounded, and in transverse rows that may be slightly irregular.

Dewlap: Large; present in both sexes, slotted (= inset), pale peach in males, brown with a cream border in females, scales large and arranged in rows, larger than throat scales and about the same size as ventrals; marginal dewlap scales crowded and about the same size as throat scales adjacent to dewlap.

Limbs and digits: Limbs short, tibial length about equal to distance from tip of snout to center of eye. Thirteen to 17 lamellae under phalanges II and III of fourth toe. Scales of limbs smooth, those of anterior surface of thigh slightly smaller than ventrals. Supradigital scales smooth.

Tail: Round non-verticillate, with a median series of widely spaced spinose scales, their apices directed posteriorly, separated from each other by about 3 to 5 smaller, smooth to weakly unicarinate dorsal caudal scales. A pair of enlarged postanal scales in males. Scales behind vent and around base of tail smooth. Four to 6 ventral rows of much enlarged unicarinate caudal scales.

Color in life: The coloration and pattern of *A. sheplani* have been given both in the diagnosis of the species and in the description of the holotype and need not be repeated in detail. The lizards are capable of limited metachrosis (they have no green phase) between very pale tan (almost white) while sleeping and brown when disturbed or active. In the pale phase there is a brown nuchal dot, a broad dark sacral U, and a median dorsal series of dark brown to black dots. An intermediate pigmental condition involves a lichenate tan-and-brown phase. The dewlap is pale peach in males, dark brown with a cream border in females; although the dewlap is well developed in both sexes, it is slightly larger in males than in females.

Comparisons. The diagnosis gives details of comparisons between *sheplani* and the three remaining species of the group (*darlingtoni, occultus, insolitus*), and these need not be repeated. However, there are some salient differences that I wish to emphasize. Of the four species, *sheplani* most closely resembles *occultus* in snout–vent length; females of both species reach a snout–vent length of 40 mm, whereas the largest male *occultus* (ASFS V5489) I have examined has a snout–length of only 35 mm; Williams and Rand (1969: 13) noted maximally sized *occultus* at 34 mm snout–vent length (sex not stated), but Williams and Rivero (1965: 7) gave 42 mm as the size of the largest *occultus* (sex not stated) examined by them. *A. sheplani* is smaller than *A. insolitus* (maximally sized male 47 mm — ASFS V22502; female 44 mm — ASFS V31614), and much smaller than *A. darlingtoni* (holotype male, 72 mm). Of the four species, only *occultus* males lack enlarged postanal scales. The spinose or tuberculate head scales, and the supratemporal line of enlarged scales which terminates in a spine, are absent in *sheplani,* as well as *occultus* and *darlingtoni;* these features are distinctive of *insolitus.* Scales between the second canthals are very numerous in *occultus* (9–14) and very many less in the other species, with *insolitus* having 2–6 (mode 4) and *sheplani*

4–6 (mode 5). *A. darlingtoni* has 5 scales between the second canthals. Loreal rows are modally 2 in *sheplani,* 3 in *darlingtoni* and in *insolitus,* and 4 in *occultus.* The supraorbital semicircles are modally separated by 3 scales (2–5) in *occultus,* by 1 row of large scales in *insolitus,* by 1 row of small scales (0–2) in *sheplani,* and by 1 row of small scales in *darlingtoni.* Scales between the interparietal and the supraorbital semicircles are modally bilaterally 4 in *occultus* (range 2–6), and 1 scale in the other species (range 0–2 in *insolitus,* 1–2 in *sheplani,* 1 in *darlingtoni*). The supraocular disks in *occultus* have no enlarged scales, whereas in *sheplani* there is 1 (occasionally 2) enlarged scale in this area, in *insolitus* 1 to 6 (mode 2), and 5 in *darlingtoni.* Scales posteriorly in contact with the rostral are 6–10 in *occultus* (mode 9), 4–7 in *insolitus* (mode 5), 4–8 in *sheplani* (mode 5), and 6 in *darlingtoni.* The canthal scales are poorly defined and very numerous (7–12; mode 10) in *occultus,* whereas all *sheplani* have 4 distinct canthals, *insolitus* modally has 4 distinct canthals (range 3–6), and *darlingtoni* has 5. There are 9–11 supralabials to the eye center in *occultus* (mode 10), 6–8 (mode 7) in *insolitus,* 7–10 (mode 8) in *sheplani,* and 7 or 8 in *darlingtoni.*

The dewlap color in *occultus* is pinkish gray, whereas that of *insolitus* varies between rich mustard, brown, orange or orange-ocher; in neither of these species is the dewlap color sexually dichromatic, whereas the dewlap is strongly sexually dichromatic in *sheplani.*

Thomas (1965: 15–16) gave a résumé of the color repertory of *occultus;* the pattern of this species consists of a dark cephalic figure or interocular trangle; dark radiating eye lines; four zones of transverse body banding (scapular, dorsal, lumbar, sacral); a single or paired lumbar spot; and a fine reticulum of dark lines which frequently appears as small ocelli. The ground color of *occultus* varies through shades of gray through olive-brown, olive, yellow-green to dirty orange, to a lichenate off-white or very light gray and black or very dark gray. In *insolitus,* the dorsum is grayish green or grayish brown, irregularly marbled, with a distinctive pale green supra-axillary crescent, a white subocular spot, and a black postorbital spot. In life, the supra-axillary crescent is extremely clear, and it, plus the black postorbital spot, are ready recognition features of the species. At night while asleep, *insolitus* may often be a very pale tan or white, very much in the fashion of *sheplani.* The coloration of *darlingtoni* in life is unknown, but Williams and Rand (1969:

11) have an excellent figure showing the basic design of the holotype. Conspicuous details of the pattern are a large dark postocular blotch and a generally transversely banded (about five fragmented bands) dorsal pattern.

One structural feature is interesting. *A. occultus* has the median dorsal scales unmodified into any sort of spines or crest scales. In *sheplani,* there are isolated spinose scales along the dorsal midline, the scales separated widely by small dorsal scales. In *insolitus,* there are low raised bosses that are covered by "rosettes" of scales, slightly larger than their surrounding scales, the bosses separated by unspecialized dorsal scales. These raised "bosses" with the rosettes of scales become slightly less conspicuous posteriorly, and on the tail are replaced by laterally compressed and spaced individual triangular scales as part of the same dorsal series. *A. darlingtoni* lacks specialized middorsal scales.

Field observations. All specimens of *A. sheplani* were taken in a very circumscribed area between 3200 and 3300 feet (976 and 1007 meters) in the Sierra de Baoruco. The immediate area where the lizards were secured is high mesic deciduous forest, somewhat modified by the cultivation of coffee and cacao. The high original forest trees have been retained as shade cover for the cultivated plants. The general aspect is rich, wet, and very well wooded. A newly constructed highway ascends the northern slope of the Sierra de Baoruco between Cabral in the Valle de Neiba and the settlements of Las Auyamas and Polo in the Baoruco uplands. At a distance of 10.4 miles (16.6 km) south of Cabral, an unpaved but quite good road takes off to the southeast of the main highway and terminates abruptly at the settlement of La Lanza. The road apparently formerly went from La Lanza to the coastal town of Paraíso, but this section is no longer passable. At a distance of between 1.9 and 2.6 miles (3.0 and 4.2 km) from the intersection, the road has been cut into a gradually sloping mountain side. Below the road there are high-canopied *cafetales* and *cacaotales;* above the road, and separated from it by a road-cut bank that varies from 2 to 10 feet (0.6 to 3.1 meters) in height, is an area of second-growth trees, saplings, shrubs, and weed and grass patches, the arborescent vegetation heavily interlaced with living and dead vines, primarily those of a purple-flowered member of the Convolvulaceae. In many places along this limited stretch of road, there are dense mats and curtains of vines; it was within and under these mats that *A. sheplani* was encountered. The species is far outnumbered by *Anolis hendersoni* Cochran, which sleeps in precisely the same situations, and one *Anolis singularis* Williams was also found sleeping syntopically with *A. sheplani.*

Sleeping sites of *A. sheplani* are bare twigs and vines within and beneath the curtains and mats of vines. The lizards sleep exposed and are easily seen since they are very pale. They are not easily disturbed by movement of the collector, jostling of the vines, or flashlight. On those rare occasions when an individual was disturbed, it opened its eyes, clutched the twig or vine more tightly, and, if pressed, moved unhurriedly away from the source of disturbance. We never saw *A. sheplani* either scurry away or drop to the ground in the fashion of other anoles when disturbed at night. Rather, their reaction to complete disturbance (for instance, touching the lizard or breaking the twig or vine to collect it) only caused the lizard to cling more tightly to its substrate. The lowest lizard was taken at a height of 3 feet, the highest 14 feet, above the ground; this gives a sleeping range of 3 to 14 feet (0.9 to 4.3 meters). It is probable that *A. sheplani* sleeps even higher on vines in the canopy, but at this location the trees in general are fairly low (perhaps 20 feet — 6.1 meters — average height) and thus the vines are low. It is significant that we never encountered *A. sheplani* below the road in this same area, despite suitable vine mats and curtains; on the lower side of the road the forest is much less disturbed and the canopy is much higher. In neighboring situations, even within a few meters, *A. cybotes, A. coelestinus* and *A. distichus* were also found sleeping.

It is instructive to compare the sleeping sites and general behavior of *A. sheplani* with that of *A. insolitus* and *A. occultus.* I have the impression that *insolitus* is an inhabitant of much less disturbed situations than *sheplani.* The known localities for *insolitus,* which now number seven, are invariably gallery forest along rivers or streams. At some localities for *insolitus,* the forest has been slightly disturbed by planting of coffee and cacao, but in general the canopy is high and dense, and vines and lianas are abundant and conspicuous (but often quite high). Consequently, sleeping sites of *insolitus* are not restricted to sheltered spots beneath vine mats or curtains. Regularly, specimens of *insolitus* have been taken completely exposed on the tips of twigs, vines, and branchlets, at heights above the ground between 2 and 25 feet (0.6 and 7.6 meters). On occasion, *A. insolitus* have been taken sleeping on green leafy shrubs rather than on bare twigs and vines. At the type locality, however, during a very heavy and continuous rain, most *insolitus* were secured in sheltered situations under vine mats or curtains, and two individuals were found sleeping on top of each other on a pendant vine. In summary, the sleeping sites of *A. insolitus* are regularly much more exposed than are those of *A. sheplani.*

Thomas (1965) and Webster (1969) have both commented upon the habits of *A. occultus* in Puerto Rico. Northeast of Guayama, Thomas reported *occultus* "sleeping at night in tangles of dead (or leafless) vines and twigs along both sides of the path, four to ten feet above the ground" on a forested hillside, and north of Sabana Grande Thomas recorded this species sleeping at heights of 4 to 15 feet (1.2 to 4.6 meters) on dead vines. Finally, south-southeast of Villa Pérez, *A. insolitus* was encountered asleep in the same sorts of situations 5 to 12 feet (1.5 to 3.7 meters) above the ground. Webster reported sleeping sites of seven *A. occultus* at a locality south of Palmer as "long, exposed twigs, . . . twigs near leaves, . . . and the upper surface of a broad, stiff leaf." Webster also located six additional *A. occultus* sleeping on living twigs near leaves, one on a long dead twig, and at the tip of a very long descending branch, and a juvenile on a dead fern. Both Thomas and Webster commented on the habit of *occultus* of clinging tightly to twigs when disturbed; this habit is shared with *A. sheplani* as noted above. The same is true of *A. insolitus;* on one occasion, we cut from the tree the small branch upon which an *insolitus* slept, and the lizard remained clinging to the branchlet during the entire operation. On another occasion, a pendant vine upon which an *insolitus* slept was deliberately broken above and below the lizard and then accidentally dropped onto the ground in leaf litter and herbaceous growth. When the vine was located, the now wide-awake *insolitus* was seen to be still clinging tightly to the vine!

Remarks. I have little doubt that *A. sheplani* is more closely related to *A. insolitus* than to *A. darlingtoni,* despite the fact that the latter species occurs on the south island along with *sheplani* (although the sole *darlingtoni* locality is removed some 310 kilometers to the west of those for *sheplani*). It is truly puzzling, considering the intensive (albeit local) collecting activity on the Hispaniolan south island in Haiti, most especially in the mountains above Port-au-Prince (Montagne Noire, Morne l'Hôpital) and in the Massif de la Hotte (Les Platons, Castillon) that no further specimens of *A. darlingtoni* have been encountered. I suspect that the habits of this species will be found to be very like those of the remaining members of the complex; if so, then nocturnal collecting with emphasis on dead vines, branches, twigs, etc., in sheltered locales may well be the secret of securing more *A. darlingtoni.* Considering the apparently very narrow ecological situations that *A. sheplani* favors, and the fact that the uplands of the Sierra de Baoruco in the Las Auyamas-Polo region have presumably been well collected since the 1920's, there is always the possibility that *A. darlingtoni* has equally stringent ecological requirements that have been overlooked or that may be very restricted in the Massif de la Hotte. Likewise, I have little doubt that *A. sheplani* will be encountered elsewhere in the Sierra de Baoruco and (or a related form) in the Massif de la Selle and its associated ranges.

The knowledge that the *darlingtoni* group of anoles occurs on both the north and south Hispaniolan islands should spur interest in ascertaining the presence of similar species of this small group in other Hispaniolan ranges. Most pertinent is the Sierra de Neiba, that range which borders the Valle de Neiba on its northern side, just as the Sierra de Baoruco borders the low-lying valley on its southern side. If *insolitus* and *sheplani* are more closely related to each other than either is to *darlingtoni,* it would seem likely that some member of this group of anoles occurs in the uplands of the intervening Sierra de Neiba. On this premise, we visited that range both during the day and at night during 1971, but to no avail. The forests are mesic and viney, altogether suitable situations for members of this group of lizards. The canopy is generally high, however, and this may make it more difficult to secure related anoles if they occur in this range. However, in similar high-canopied forests south of El Río in the Cordillera Central, *A. insolitus* was easily observed. It may well be that there is no member of the *darlingtoni* group in the Sierra de Neiba, but this range is so poorly known herpetologically that one cannot with certainty dismiss the absence of a related species there.

The elevational distributions of the four members of the *darlingtoni* complex are interesting. *A. occultus* in Puerto Rico is known to occur between elevations of 2300 and about 4389 feet (702 and 1338 meters), whereas the known altitudinal ranges of the other species are: *darlingtoni,* 5000 feet (1525 meters); *sheplani,* 3200–3300 feet (976–1007 meters); and *insolitus,* 3500–5800 feet (1068–1769 meters). Although the data on *darlingtoni* and *sheplani* are limited, *insolitus* seems to reach higher elevations in the Cordillera Central than any species does elsewhere. This may at least in part be due to the fact that no mountains in Puerto Rico or the Sierra de Baoruco reach such high elevations as do the mountains within the area known to be inhabited by *insolitus.*

Williams and Rand (1969: 9) noted that "It would be a possible argument against the close affinity of the two species that *darlingtoni* (72 mm) is approximately twice the snout–vent length of *insolitus* (33 mm). Differences in size between closely related species, particularly if they are sympatric, are not unusual, but as far as known, these two species are widely allopatric, and the size difference is extreme." More recently collected and larger numbers of *A. insolitus* show that the supposed extreme difference in size (= snout–vent length) between *darlingtoni* and *insolitus* is not so striking as Williams and Rand supposed. In fact, *insolitus,* which reaches a maximum known snout–vent length of 47 mm (not 33 mm) but which is nonetheless still smaller than *darlingtoni,* rather bridges the size gap between smaller *occultus* and *sheplani* and larger *darlingtoni.* The size discrepancy for members of the complex, which Williams and Rand felt might argue against relationships among these lizards, is not so striking as they supposed.

Specimens examined. Anolis occultus: PUERTO RICO, 20.9 km NNE Guayama, 2300 feet (702 meters) (ASFS V4891–92, V4901, V5017–18); 13.7 km N Sabana Grande, 2800 feet (854 meters) (ASFS V5489–91, V5494); 13.7 km S Palmer (ASFS V6662–65); 10.6 km SSE Villa Pérez, 3400 feet (1037 meters) (ASFS V6196–97).

Anolis insolitus: REPUBLICA DOMINICANA, *La Vega Province,* La Palma, 14 km E El Río, 3500 feet (1068 meters) (ASFS V18739, V18917–19, V22546–53, V31705–10); 1.9 mi. (3.0 km) SW El Río, 3900 feet (1190 meters) (ASFS V31656–63); 16 km SE Constanza, 5250 feet (1601 meters) (ASFS V22502–05); 16.4 km SE Constanza, 5500 feet (1678 meters) (ASFS V31614); 18 km SE Constanza, 5800 feet (1769 meters) (ASFS V19096); 18.5 km SE Constanza, 5800 feet (1769 meters) (ASFS V31581–82). *Peravia Province,* 6.5 mi. (10.4 km) NW La Horma, 5400 feet (1647 meters) (ASFS V31933–37, V31973–74); 8.1 mi. (13.0 km) NW La Horma, 5800 feet (1769 meters) (ASFS V31927–28).

Anolis darlingtoni: HAITI, *Dépt. du Sud,* Roche Croix, Massif de la Hotte, ca. 5000 feet (1525 meters) (MCZ 38251).

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THE LARVA OF *SPHINDOCIS DENTICOLLIS* FALL AND A NEW SUBFAMILY OF CIIDAE (COLEOPTERA: HETEROMERA)

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Abstract. The larva of *Sphindocis denticollis* Fall is described, and its biology is briefly discussed. A new subfamily of Ciidae — the Sphindociinae — is proposed for *Sphindocis* and is formally characterized, while the Ciidae and Ciinae are redefined. Speculations are made concerning the phylogenetic relationships of the family Ciidae.

The monotypic genus *Sphindocis* Fall is based on a very interesting fungus-feeding beetle (*S. denticollis*) that is known only from the Transition Zone forests of the northern California coast. The genus was originally placed in the family Ciidae (Fall, 1917), but it was recently removed from that family and tentatively placed in the Tetratomidae (Lawrence, 1971). At the suggestion of R. A. Crowson, I made a more detailed study of the *Sphindocis* larva, comparing it and the adult with various Ciidae, Tetratomidae, Pterogeniidae, and related Heteromera. As as result, I have come to the conclusion that *Sphindocis* represents the closest living relative or sister group of the Ciidae and should either be returned to that family or form the basis for a new group of equal rank. The former alternative appears more reasonable, since the number of families in the Heteromera is already excessive. The following treatment includes a description of the *Sphindocis* larva, the proposal of a new subfamily for the inclusion of this genus, and a recharacterization of the family Ciidae and subfamily Ciinae.

The larval description is based on more than 50 specimens collected with adults in the fruiting bodies of *Trametes sepium*

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Berkeley growing on dead branches of madrone (*Arbutus Menziesii*) at the following localities in California: Alpine Lake, Marin County; 1 mi. N Piercy, 2 mi. N Piercy, 3 mi. S Leggett, and 4 mi. W Leggett, Mendocino County. Another eight specimens were collected without adults in a fruiting body of *Poria cinerascens* (Bresadola) Saccardo and Sydow growing on a Douglas fir (*Pseudotsuga Menziesii*) log at Alpine Lake. A single pupa was dug out of madrone wood beneath a fruiting body, which may indicate that the beetles require the woody substrate for pupation.

Most of the terms used in the larval description are those found in standard works, such as Böving and Craighead (1931) and van Emden (1942). For the three labial sclerites, I have used the terms prementum, mentum, and submentum, although Anderson (1936) has indicated that these are not homologous in all groups. Terminology for the ventral thoracic sclerotizations follows Watt (1970), while various other terms have been taken from Crowson (1955), Glen (1950), Rozen (1958, 1960), St. George (1924), and Snodgrass (1935).

I wish to thank H. B. Leech and the California Academy of Sciences, San Francisco, for the loan of specimens; J. T. Doyen for collecting adults and larvae of *Sphindocis;* and R. A. Crowson and E. Mayr for their encouragement.

DESCRIPTION OF THE MATURE LARVA OF *Sphindocis denticollis* Fall

Body elongate and subcylindrical, lightly sclerotized except for head, anterior part of prothoracic tergum, and pygidium (upper part of ninth abdominal tergum). Length about 5 mm; width about 0.7 mm.

Head (Figs. 1–3) exserted, obliquely prognathous, subglobular, strongly convex dorsally, except for a broad, shallow concavity (c) extending from the middle of the epicranial stem to the upper part of the frontoclypeal triangle (fc); heavily sclerotized and yellowish brown in color, with fairly coarse and irregular punctation; vestiture consisting of numerous short setae and several longer ones, the origins of which are shown in Figures 1–3. Epicranial stem (es) about half as long as head width; frontal arms (fa) somewhat V-shaped and extending to antennal ridges (ar), which conceal antennal insertions; endocarina absent. Frontoclypeal area (fc) bearing two parallel, transverse sulci (ts) near epistomal margin (em). Epicranial

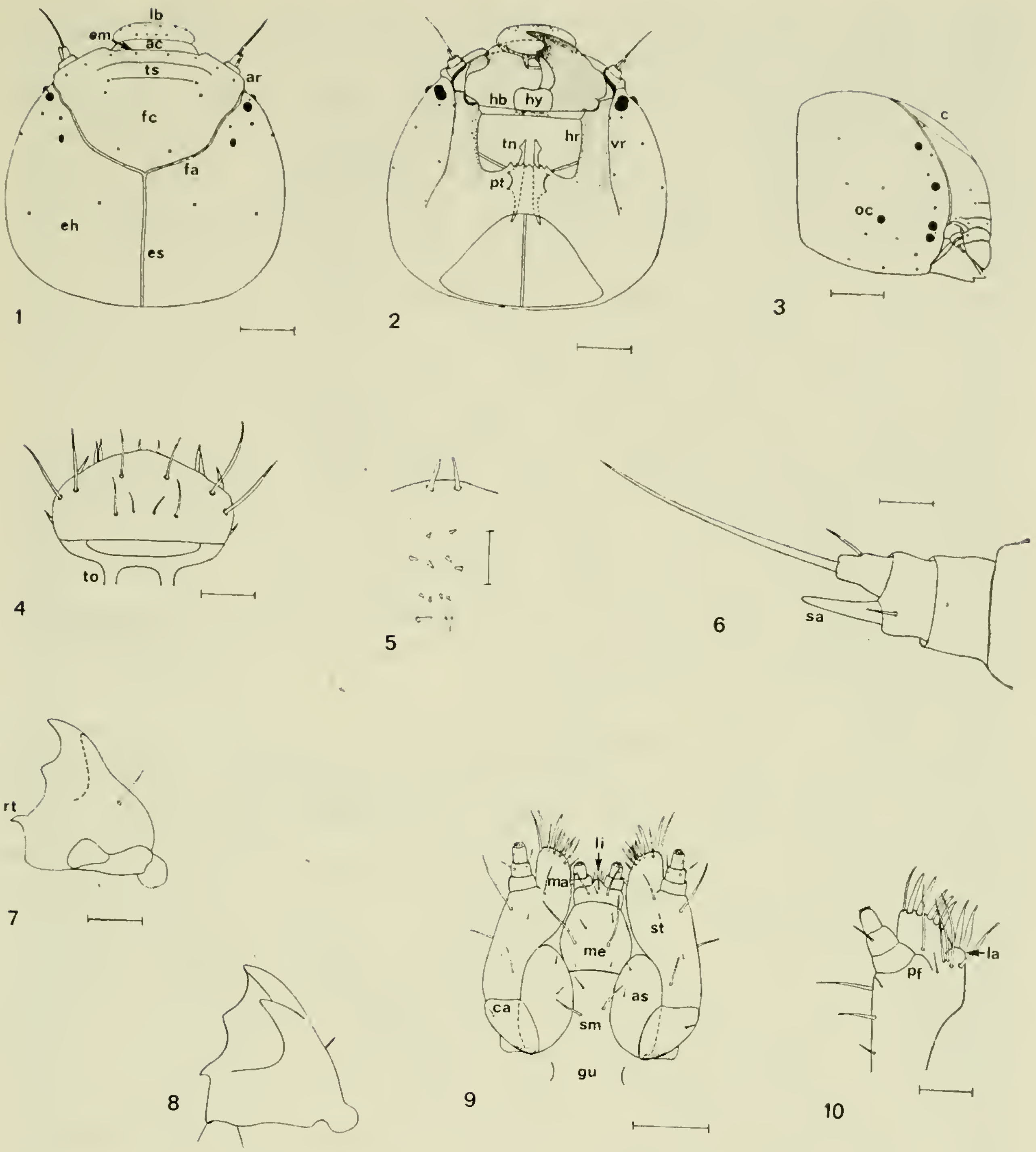
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Plate 1

Figures 1–10. *Sphindocis denticollis* Fall, larva (1 line = 0.125 mm for 1–3, 9; 0.063 mm for 4, 7, 8, 10; 0.025 mm for 5, 6). Fig. 1. Head capsule, dorsal view, mandibles and ventral mouthparts removed (dots = setal origins). Fig. 2. Head capsule, ventral view, right mandible and ventral mouthparts removed. Fig. 3. Head capsule, lateral view. Fig. 4. Labrum-epipharynx, dorsal view. Fig. 5. Epipharynx, median portion. Fig. 6. Left antenna, lateral view. Fig. 7. Right mandible, dorsal view. Fig. 8. Left mandible, ventral view. Fig. 9. Ventral mouthparts and gular region, ventral view. Fig. 10. Apex of left maxilla, dorsolateral view.

halves (eh) each bearing a ventral ridge (vr) which extends posterad from mandibular articulation, parallel to the hypostomal ridge (hr), and forms with the latter a support for the ventral mouthparts, which are large and protracted. Ocelli (oc) 5 in number, arranged as in Figure 3. Anteclypeus (ac) a short, lightly sclerotized band. Labrum (lb) transversely oval, with setae and spines as in Figure 4; epipharynx with 4 median groups of very short setae or sensillae (Fig. 5); tormae (to) symmetrical, joined posteriorly by a narrow bridge. Antenna (Fig. 6) fairly short, less than 1/10 as long as head width, 3-segmented, segments about equal in length, II slightly narrower than I and bearing a sensory appendix (sa) that is longer than III and ventral to it, III about half as wide as II and bearing a terminal seta almost five times its length; antennal insertion separated from the mouth cavity by a narrow bar. Gula (gu) not well defined; gular sutures absent and no suture between gula and submentum (sm). Posterior tentorial pits (pt) and tentorium (tn) as in Figure 2.

Mandibles (Figs. 7 and 8) symmetrical, large and wedge-shaped, with two apical teeth of unequal lengths, an obtuse tooth on the cutting edge, and a lightly sclerotized retinaculum (rt); mola absent; a seta located on the dorsal surface near the middle of the lateral edge. Maxillae (Fig. 9) free almost to base of mentum; mala (ma) obliquely rounded, its apex armed with 5 stout spines and several finer setae; inner edge of mala (Fig. 10) bearing a dorsal laciniar lobe (la), located at the level of the palpifer (pf) and bearing 2 stout apical spines and several long setae at base; stipes (st) elongate; cardo (ca) subtriangular; a large, articulating sclerite (as) between stipes and submentum; palp 3-segmented. Labium with a short prementum, a subquadrate mentum (me), and a submentum (sm), which is raised above the gula but is not separated from it; ligula (li) short and rounded, bearing 4 setae at apex; palp 2-segmented. Hypopharynx (hy) subquadrate, without a sclerome; hypopharyngeal bracon (hb) lightly sclerotized except at base of hypopharynx.

Prothorax (Fig. 11) slightly longer than meso- or metathorax, its tergum (prt) well developed and extending onto lateral surfaces, heavily pigmented anteriorly, becoming very lightly pigmented posteriorly, with a median ecdysial suture; vestiture consisting of numerous short setae and 3 transverse rows of setae consisting of 12 (anterior edge), 8 (anterior third), and 10 (posterior third) setae; sternum consisting of a large, tri-

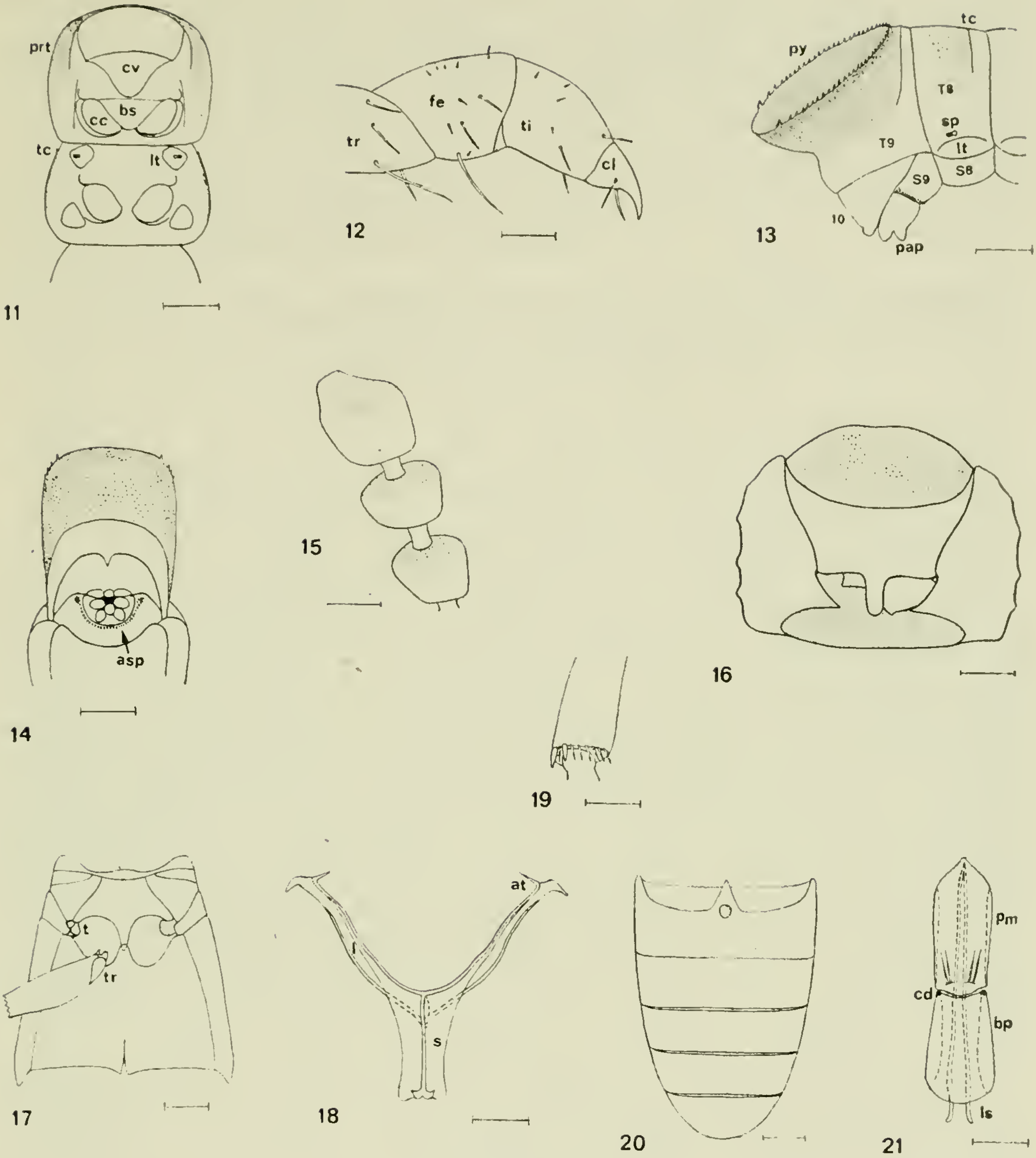
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Plate 2

Figures 11–14. *Sphindocis denticollis* Fall, larva (1 line = 0.063 mm for 12; 0.250 mm for 11, 13, 14). Fig. 11. Prothorax and mesothorax, ventral view, legs removed. Fig. 12. Prothoracic leg, coxa and part of trochanter not shown. Fig. 13. Apex of abdomen, lateral view. Fig. 14. Apex of abdomen, ventral view. Figures 15–21. *Sphindocis denticollis* Fall, adult male (1 line = 0.063 mm for 15, 19; 0.250 mm for 16, 17, 20; 0.125 mm for 18, 21). Fig. 15. Antennal club. Fig. 16. Prothorax, ventral view, right coxa removed. Fig. 17. Meso- and metathorax, ventral view, left mesocoxa and metacoxae removed. Fig. 18. Metendosternite, dorsal view. Fig. 19. Apex of protibia. Fig. 20. Abdomen, ventral view. Fig. 21. Aedeagus, ventral view.

angular cervicosternum (cv), a triangular basisternum (bs), and vaguely defined sternellum, episternum, and epimeron; coxal cavities (cc) large and obliquely oval, separated by a little less than ¼ their greatest diameter. Mesothoracic tergum less extensive than that of prothorax and lightly pigmented except for a transverse carina (tc) at the anterior fifth; several long setae scattered on shield; each side with two laterotergites (lt), the anterior of which bears a biforous spiracle (sp) with the air tubes facing dorsad; sternal areas not well defined, coxae slightly smaller and broader than those of prothorax. Metathorax similar in structure, but with no spiracle on the anterior laterotergite. Legs about equal in size, with a large conical coxa, triangular trochanter (Fig. 12, tr), the femur (fe) and tibiotarsus (ti) about equal in length, and the claw (cl) bearing two setae.

Abdominal segments 1 to 8 slightly convex dorsally and strongly so ventrally; tergal shields lightly pigmented, each with an anterior carina and several long setae; each side with a single laterotergite (Fig. 13, lt), just above which is the spiracle with the air tubes facing posterad. Ninth abdominal segment (Figs. 13 and 14) longer than those preceding it, with a large tergum bearing a heavily pigmented, circular, concave, declivous pygidium (py), lined along ¾ of its circumference with saw-like teeth; ninth sternum reduced in size, bearing at its apex a row of anteriorly projecting asperites (asp); tenth tergum lunate, partly separating ninth tergum and sternum, bearing 3 papillae (pap) at its apex; tenth sternum reduced and pygopod-like, bearing 5 papillae in front of anal opening (Fig. 14).

This larva differs from that of any other known ciid in lacking an endocarina and having 3-segmented antennae, a maxillary articulating sclerite, biforous spiracles, and subanal asperites on the ninth sternum. The presence of an endocarina has never been noted for the Ciidae, probably because it is directly beneath the epicranial stem and does not extend anterad of the frontal arms, as it does in various other Heteromera. The epicranial stem in *Sphindocis* is an ecdysial line, whereas in other Ciidae it coincides with an internal ridge. The reduced antennal segmentation in most ciid larvae represents a fusion of the last two segments. Symmetrical mandibles also occur in other Ciidae, but asymmetry appears to be the more common condition. Biforous spiracles appear to be unique to *Sphindocis,* but a peculiar type of accessory air tube has been observed in at least one other ciid (unpublished). The concave pygidium of *Sphindocis,* which occurs in other Ciidae, such as *Cis melliei* (Coquerel, 1849), in the tenebrionid genus *Meracantha* (Hyslop, 1915), and in various other substrate-dwelling beetle larvae, represents a type of defensive adaptation, which Wheeler (1928) termed phragmosis. The fruiting body of *Trametes sepium* is often resupinate with a fairly thin context, and the concave and heavily sclerotized pygidium in *Sphindocis* serves to block the shallow larval tunnel against predators or parasites.

CHARACTERIZATION OF THE FAMILY CIIDAE AND ITS SUBFAMILIES

Ciidae Leach

With the general characters of the Polyphaga: Cucujoidea.

Adult. Form variable, usually oval to elongate, convex. Size 0.5–6.0 mm. Head globular, without neck, often strongly declined, partly concealed by pronotum, without stridulatory files. Eye oval, entire, fairly coarsely facetted. Frontoclypeal area with a distinct suture, often raised in males to form a ridge, horns, or tubercles. Antennal insertion concealed from above by frons. Antenna 8- to 11-segmented, with a 2- or 3-segmented club, club segments often with multi-pronged sensillae (absent in *Sphindocis*). Mandible bidentate, with a simple cutting edge and a quadrangular mola without ridges or tubercles. Maxilla with an articulated lacinia and 2-segmented galea (*Sphindocis*) or a fixed lacinia and 1-segmented galea (Ciinae), palp 4-segmented, the terminal segment not securiform. Labium with ligula reduced, palp 3-segmented. Pronotum margined laterally and posteriorly, anterior edge usually produced forward, sometimes bearing horns in male. Prosternum variable, long or short, concave to carinate, coxae globose or transverse, sometimes projecting, contiguous to broadly separated, without internalized lateral extensions, trochantin usually concealed; procoxal cavities open internally, narrowly open or closed externally (posteriorly). Elytra not striate, humeri tuberculate, epipleura very narrow, extending almost to apex. Scutellum small and subtriangular, sometimes absent. Wing venation often reduced, subcubital fleck present, anal region with four veins (*Sphindocis*) or only one (Ciinae). Mesosternum transverse, sometimes extremely reduced, coxae globose and narrowly separated, coxal cavities not closed outwardly by sterna, trochantins exposed or not. Metasternum subquadrate, with or without median suture, without coxal lines, coxae narrow, transverse, subcontiguous. Metendosternite with a long median stalk (*Sphindocis*) or none (Ciinae), anterior tendons arising near the apices of the lateral arms. Tarsal formula in both sexes 4–4–4 (occasionally 3–3–3), tarsi simple, the first three segments small and subequal, terminal segment elongate, claws simple. Trochanters oblique, completely (Ciinae) or only partly (*Sphindocis*) separating coxa from femur. Tibial spurs usually absent; 2 reduced spurs in *Sphindocis.* Outer edge of protibia often expanded and modified at apex. Abdomen with 5 visible sternites, the first 2 (III and IV) connate (*Sphindocis*) or not (Ciinae). First visible sternite (III) without coxal lines, often with a median pubescent fovea in male. Aedeagus of inverted heteromeroid type, with ventral tegmen and dorsal median lobe.

Larva. Body elongate and subcylindrical, lightly sclerotized, except at anterior and posterior ends. Head subglobular, obliquely prognathous, with well-developed epicranial stem and Y-shaped frontal arms, endocarina present (Ciinae) or not (*Sphindocis*); ventral epicranial ridge present behind mandibular articulation. Ocelli usually 5, occasionally fewer or none. Antennal insertion concealed from above and separated from mouth cavity by a narrow bar. Antenna short, 2- or 3-segmented, with a long sensory appendix on segment II and a very long terminal seta. Gular area short, sutures present or absent. Mandibles large and wedge-shaped, usually somewhat asymmetrical, with 2 apical teeth, a simple cutting edge, often with a lightly sclerotized retinaculum, mola usually absent. Maxilla free at least to middle of mentum, with a narrow articulating membrane (Ciinae) or a large articulating sclerite (*Sphindocis*) between stipes and submentum; mala obliquely rounded, inner edge with a dorsal laciniar lobe; palp 3-segmented. Labium with short prementum, subquadrate mentum, and elongate submentum, the last separated from gula by suture or not; ligula short and rounded, with 2 or 4 setae; palp 2-segmented. Hypopharynx without sclerome. Thoracic terga well developed and extending onto sides; prothorax slightly larger than meso- or metathorax; prosternum with a large triangular cervicosternum; procoxae large and fairly close together; spiracle annular (Ciinae) or biforous (*Sphindocis*), located on anterior laterotergite of mesothorax. Legs fairly short and broad, subequal; claw with 2 setae. Abdominal spiracles located above laterotergites. Ninth tergum variously modified, usually heavily sclerotized and with urogomphi; tenth sternum reduced and pygopodlike; anal opening surrounded by several papillae.

Sphindociinae, New Subfamily

Adult. Antenna 11-segmented, with 3-segmented club (Fig. 15); club segments without multi-pronged sensillae. Maxilla with an articulated lacinia and a 2-segmented galea. Pronotum (Fig. 16) with lateral margins broadly crenulate, so that several round teeth are formed; procoxal cavities with a slight lateral extension, which may expose part of trochantin. Mesocoxal cavities (Fig. 17) with exposed trochantins (t). Metendosternite (Fig. 18) with a long stalk (s), a narrow lamina (l), and the anterior tendons (at) near the apices of lateral arms. Hindwing with well-developed anal region, bearing 4 veins and a wedge cell. Trochanter (Fig. 17, tr) of heteromeroid type, obliquely joined to femur so that the latter is in direct contact with coxa at one point. Tibial apices (Fig. 19) simple, with 2 reduced spurs. Abdominal sternites III and IV connate (Fig. 20), III with a median pubescent fovea in male. Aedeagus (Fig. 21) with a large basal piece (bp), with two apical condyles (cd), a well-sclerotized ventral paramere (pm) with 2 pairs of setae near its base, and a membranous median lobe with 2 lateral struts (ls).

Larva. Head without endocarina, with 5 ocelli. Antenna 3-segmented. Mandibles symmetrical, without mola and with lightly sclerotized retinaculum. Maxilla free almost to base of mentum, with a large articulating sclerite between stipes and submentum. Spiracle biforous. Ninth tergum bearing a concave pygidium surrounded by saw-like teeth; ninth sternum bearing a row of asperites.

Ciinae Leach

Adult. Antenna 8- to 10-segmented, with a 2- or 3-segmented club; club segments with at least 4 multi-pronged sensillae. Maxilla with a reduced and fixed lacinia and a 1-segmented galea. Pronotum with lateral margins never broadly crenulate or toothed; procoxal cavities without lateral extension, trochantin always concealed. Mesocoxal cavities with trochantins concealed. Metendosternite with median stalk very short and broad, so that arms may appear to arise independently. Hindwing with reduced anal region bearing a single vein. Trochanter of normal type, oblique but completely separating coxa and femur. Tibial spurs absent on all legs, apices of tibiae, especially protibiae, variously expanded and modified. Abdominal sternites free, III often with a median pubescent fovea in male. Aedeagus with a small basal piece, without condyles, paramere variously modified at apex but without basal setae, and median lobe sclerotized and without lateral struts.

Larva. Head with endocarina, ocelli 5 or less. Antenna 2-segmented. Mandibles often asymmetrical, with or without mola and retinaculum. Maxillae free to about middle of mentum, without an articulating sclerite at its base. Spiracles annular. Ninth tergum variously modified, usually with two urogomphi; ninth sternum without asperites.

This subfamily includes all members of the family except *Sphindocis.*

DISCUSSION

The major justification for uniting *Sphindocis* and the Ciidae is the joint possession by the two groups of at least one feature — the distinctive laciniar lobe of the larval maxilla — which is certainly unique and derived. This particular type of structure is found in no other cucujoid beetle, and it is sufficiently complex and similar in the two groups to make convergence unlikely. There is no reason to believe that the cleft malar apex of the Zopheridae, Cephaloidae, and Synchroidae, or the various teeth, spines, or hooks (to which the word uncus is often applied) of *Anaspis,* the Oedemeridae, and various other Heteromera are homologous to this laciniar lobe. The loss of the mandibular mola and of the hypopharyngeal sclerome in the larva are also derived features, but it would be difficult to demonstrate their uniqueness. The lightly sclerotized and tooth-like "retinaculum" of the larval mandible appears to be unique in the Heteromera, but similar structures occur in a number of Clavicornia, suggesting that the character may be primitive. In the adult stage, the reduction of the ligula and the presence of an abdominal fovea in the male may both represent synapomophic conditions, but most other adult characters are shared by one or more Heteromera. The abdominal fovea is rare in this section of the Cucujoidea, although some Mycteridae and at least one mycetophagid have abdominal tufts or patches of hairs in the male. Foveae similar to those of ciids, however, do occur in certain Erotylidae among the Clavicornia (Delkeskamp, 1959).

The erection of a new subfamily for *Sphindocis* is based on numerous differences between this genus and all of the remaining ciids. In larval Ciinae, the antennae are reduced to two segments, an endocarina is present, the maxillary articulating area is reduced to a narrow membrane, the spiracles are annular without a pair of contiguous air tubes, the ninth sternite lacks a row of asperites, and the gula and submentum are not fused, while in the adults of this subfamily, the antennae always have less than 11 segments, the club segments bear multi-pronged sensillae, the galea has only a single segment, the lacinia is not articulated, the anal region of the hindwing has only a single vein, the pro- and mesotrochantins are concealed, the trochanters are not heteromeroid, the tibial spurs are lacking, the abdominal sternites are free, and the median lobe of the aedeagus is sclerotized. Most of these characters are derived and several are obviously associated with reduction in size (hindwing, antennal segments of adult and larva, adult maxilla). The development of large and complex hygroreceptor sensillae on the antennal club probably represents an improvement in the ability to locate fungus sporophores, while the formation of a larval endocarina, reduction of the maxillary articulating area, the further enclosure of the pro- and mesocoxae, and the loss of tibial spurs may have been associated with the utilization of a tougher fungus substrate.

The relationships of the Ciidae to other heteromerous families are still somewhat obscure, and a detailed discussion must await a study now in progress on adult and larval Heteromera. Crowson (1966) suggested that the Ciidae, along with the Pterogeniidae, Tetratomidae, and Mycetophagidae, might be direct offshoots from a biphyllid-byturid type of heteromeran ancestor, and that the Pterogeniidae might represent the sister group of the Ciidae. I have agreed basically with Crowson's views (Lawrence, 1971), while allowing for the possibility that the ciids have evolved directly from a clavicorn ancestor, perhaps related to *Cryptophilus* or *Setariola* in the Languriidae.

The Pterogeniidae resemble ciids both as adults and larvae, but the similarities may be due to the fact that both groups inhabit the woodier fungi. Adult pterogeniids differ from the Ciidae in having filiform antennae, securiform maxillary palps, a 5–5–4 tarsal formula, internally closed procoxal cavities, and distinct lateral lobes on the aedeagus. The larvae of *Pterogenius* and *Histanocerus,* which are being described elsewhere, differ from those of ciids in having a characteristically curved epicranial stem, an extensive mandibular mola with transverse ridges, a well-developed and molar-like hypopharyngeal sclerome, and no laciniar lobe on the maxilla.

The row of asperites at the apex of the ninth sternite in the *Sphindocis* larva is found outside the group only in the genus

Prostomis, which has been placed in a separate family of uncertain affinities. The row of asperites in the larvae of Pythidae, Pyrochroidae, and Othniidae is always at the base of the ninth sternite and is apparently not homologous to that of *Sphindocis.* The Prostomidae differ from ciids in having closed front and middle coxal cavities in the adult and a simple mala, well-developed mola, and hypopharyngeal sclerome in the larva.

The Tetratomidae have also been considered as a possible sister group of the Ciidae, and certain characters of both adult and larva tend to support this hypothesis. Adults of the Tetratomidae (excluding *Mycetoma,* removed by Crowson, 1966, and Viedma, 1966) and the related Mycetophagidae are similar to ciids in having internally and externally open procoxal and laterally open mesocoxal cavities, while the pisenine tetratomid *Eupisenus elongatus* (LeConte) bears a striking superficial resemblance to *Sphindocis.* The procoxal cavity in all tetratomids has a distinct lateral extension that exposes the trochantin; in *Sphindocis* there is a slight extension of the cavity, while in the Ciinae it is absent. The hindwing of *Sphindocis* is similar to that of tetratomids in having a wedge cell and subcubital fleck and differs in having four rather than five anal veins, while the metendosternite is essentially of the tetratomid type with a reduced lamina. In the Ciinae, both the hindwing and the metendosternite have undergone extreme reduction and modification.

The male genitalia of the Tetratomidae are variable, and Miyatake (1960) has described and illustrated two major types: that of *Pisenus,* with the basal piece ventral and bearing two ventral accessory lobes in addition to the parameres, which are free; and that of the Tetratomini, with the basal piece dorsal and bearing only parameres, which are at least partly fused together. In the genus *Penthe* (Penthini) the genitalia are of the tetratomine type, but in *Eupisenus,* a distinctive type occurs with the basal piece ventral and the parameres fused into a single piece notched at the apex; moreover, this single paramere bears near the base two clusters of six or seven setae, which are in the same positions as the two pairs of setae in *Sphindocis.* The median lobe is also like that of *Sphindocis* in being membranous with lateral struts that meet at the apex.

The larvae of Tetratomidae are also quite variable, but they differ consistently from those of Ciidae in having lyre-shaped frontal arms and no laciniar lobe on the maxilla. The mandible of *Pisenus* resembles that of the Mycetophagidae in having a mola with transverse ridges grading into tubercles or asperites on the ventral surface (Hayashi, 1971; 1972). In *Eupisenus,* the mola is simple and concave and is bordered by two rows of teeth that grade into tubercles both dorsally and ventrally. In the Tetratomini (Crowson, 1964) the mola is further reduced with only three or four teeth, while in *Penthe* there is no mola. The hypopharyngeal sclerome, which can often be correlated with molar development, is well developed and tooth-like in *Pisenus,* consists of a transverse band in *Eupisenus* and the tetratomines, and is barely sclerotized in *Penthe.* It would not be difficult to derive the simple mandible and unsclerotized hypopharynx of the Ciidae from a form like *Eupisenus,* and it is also possible that the "retinaculum" of the Ciidae represents a remnant of the molar teeth in tetratomids, rather than a carry-over of the clavicorn retinaculum.

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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE GENUS *LOPHODOLOS* (FAMILY ONEIRODIDAE)

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Abstract. The genus *Lophodolos* of the family Oneirodidae is reviewed on the basis of all known material. Two species are recognized, *L. acanthognathus* Regan and *L. indicus* Lloyd. *Lophodolos dinema* Regan and Trewavas is considered a junior synonym of *L. indicus* Lloyd. The tentative distribution of each species is plotted and a key to the species of the genus is provided.

INTRODUCTION

The genus *Lophodolos* was erected by Lloyd (1909a) to include a single species, *L. indicus,* on the basis of a specimen collected from the Indian Ocean by the Royal Indian Museum Survey Ship Investigator. Since that time three additional species have been described: *L. acanthognathus* Regan (1925), to which have been referred more than 60 specimens from the Atlantic and western Pacific oceans; *L. lyra* Beebe (1932), synonymized with *L. acanthognathus* by Regan and Trewavas (1932); and *L. dinema* Regan and Trewavas (1932), represented by a single specimen from the South China Sea.

The number of female specimens of *Lophodolos* has doubled since the appearance of Bertelsen's (1951) monograph on the Ceratioidei. In spite of extensive information gained from this increase in material, taxonomic study of the genus is by no means complete. Metamorphosed males are unknown; thus, species are based only on females. The separation of species is based on only a few characters, the most important being the morphology of the esca and the length of the illicium. Differences in these two characters merge in specimens less than 25 mm standard length, making differentiation particularly difficult. Nevertheless, the material presently known appears to represent only two forms: *L. acanthognathus* Regan (1925) and *L. indicus* Lloyd (1909a).

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METHODS AND MATERIALS

Standard lengths (SL) were used throughout. Measurements were taken on the left side of the fish whenever possible and rounded to the nearest 0.5 mm in specimens greater than 20 mm, and to the nearest 0.1 mm in specimens less than 20 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the escal bulb, excluding escal appendages. Terminology used in describing the various parts of the angling apparatus follows that of Bradbury (1967). Definitions of terms used for the different stages of development follow those of Bertelsen (1951: 10–11).

Locality data is given for primary type material only. Complete locality data for all specimens examined may be obtained by writing to the author.

The generic diagnosis (much of which is taken from osteological evidence presented elsewhere: Pietsch, 1974) and description are based on 98 metamorphosed females ranging from 6.0 to 77.0 mm (metamorphosed males are unknown). Larvae were described by Bertelsen (1951: 106). Study material is deposited in the following institutions:

BMNH	British Museum (Natural History), London.
BOC	Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University.
BZM	University of Bergen Zoological Museum.
CAS	California Academy of Sciences, San Francisco.
FMNH	Field Museum of Natural History, Chicago.
GNM	Natural History Museum of Göteborg.
IMC	Indian Museum, Calcutta.
ISH	Institut für Seefischerei.
LACM	Los Angeles County Museum of Natural History.
MCZ	Museum of Comparative Zoology, Harvard University.
NIO	National Institute of Oceanography, Surrey, England.
NYZS	New York Zoological Society.

ROM	Royal Ontario Museum.
SIO	Scripps Institution of Oceanography, La Jolla.
SU	Stanford University (collections now housed at the California Academy of Sciences, San Francisco).
UMML	University of Miami Marine Laboratory.
USNM	United States National Museum, Washington.
ZMUC	Zoological Museum, University of Copenhagen.

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I thank Erik Bertelsen and Karel F. Liem for critically reading the manuscript and offering valuable suggestions. Thanks are also due the following persons and their institutions for making material available: Robert J. Lavenberg and Jerry Neumann (LACM); Erik Bertelsen and Jørgen Nielsen (ZMUC); Gerhard Krefft (ISH); Richard H. Rosenblatt (SIO); W. B. Scott (ROM); William N. Eschmeyer and Tomio Iwamoto (CAS); Alwyne Wheeler (BMNH); C. Richard Robins (UMML); Nigel Merrett and Julian Badcock (NIO); Robert H. Gibbs, Jr. (USNM); Robert K. Johnson (FMNH); Thomas A. Clarke, Hawaii Institute of Marine Science, University of Hawaii; and Michel Legand, Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia. A. G. K. Menon of the Zoological Survey of India, Calcutta, kindly provided information and a sketch of the esca of the holotype of *Lophodolos indicus*. Finally, I thank Patricia Chaudhuri for the fine illustrations.

SYSTEMATICS

Genus ***Lophodolos*** Lloyd, 1909a

Lophodolos Lloyd, 1909a: 167 (type species *Lophodolos indicus* Lloyd, 1909a, by original designation and monotypy). Fowler, 1936: 1337, 1339–1340, 1365, fig. 560 (brief description after Regan, 1926; in key). Pietsch, 1974: in press (osteology; relationships).

Lophodolus (emended or erroneous spelling of *Lophodolos* by various authors).

Oneirodes Murray and Hjort, 1912: 104, fig. 90 (in part; erroneous designation; type species *Oneirodes eschrichtii* Lütken, 1871, by original designation and monotypy).

Lophodulus (erroneous spelling of *Lophodolos* by various authors).

Diagnosis. The genus *Lophodolos* is distinguished from all other genera of the family Oneirodidae by the following characters: dorsal profile of frontal bones concave; ventromedial extensions of frontals absent; posterior end of frontal in contact with respective prootic; pterosphenoid absent; pterygiophore of illicium emerging between or behind sphenotic spines; symphysial and sphenotic spines extremely well developed; medial ends of hypobranchials II (as well as hypobranchials III) approaching each other on the midline (see Pietsch, 1974: in press).

In addition, *Lophodolos* is unique in having the following combination of characters: snout short, mouth large, cleft extending past eye; vomerine teeth absent; anterior end of pterygiophore of illicium exposed, its posterior end concealed under skin; articular spines present, quadrate spine larger than mandibular spine; angular spine present; pharyngobranchials I and II absent; pectoral lobe short and broad, shorter than longest rays of pectoral fin; operculum bifurcate; suboperculum slender throughout length, its upper end tapering to a point, its lower end rounded, with a small anterior projection in some adolescent specimens; skin naked, covering caudal fin to some distance from fin base.

Description. Body relatively long, slender, not globular; jaws equal anteriorly; lower jaw with an unusually long symphysial spine; oral valves well developed, lining inside of both upper and lower jaws; two nostrils on each side at end of a single short tube; labial cartilage well developed (Pietsch, 1972a: 31); angular bone terminating as a well-developed spine; eye subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated just posteroventrad to pectoral lobe; skin naked (embedded dermal spines cannot be detected microscopically in cleared and stained specimens); lateral line papillae as described for other oneirodids (Pietsch, 1969, 1972b); ovaries paired; pyloric caeca absent.

Illicium length 11.1 to 138.0 percent of SL, becoming longer proportionately with growth (Fig. 1); anterior end of pterygiophore of illicium exposed, emerging on head between or behind sphenotic spines, its posterior end concealed under skin; esca with a pair of unpigmented, bilaterally placed appendages arising from distal surface.

Teeth slender, straight, all depressible, and weakly set (easily damaged or lost), in overlapping sets as described for other oneirodids (Pietsch, 1972b: 5, fig. 2); teeth in lower jaw larger and more numerous than those in upper jaw; number of teeth in lower jaw 200 to 280 (based on five specimens, 57.0–77.0 mm); pharyngobranchial II absent; pharyngobranchial III well developed and bearing numerous teeth.

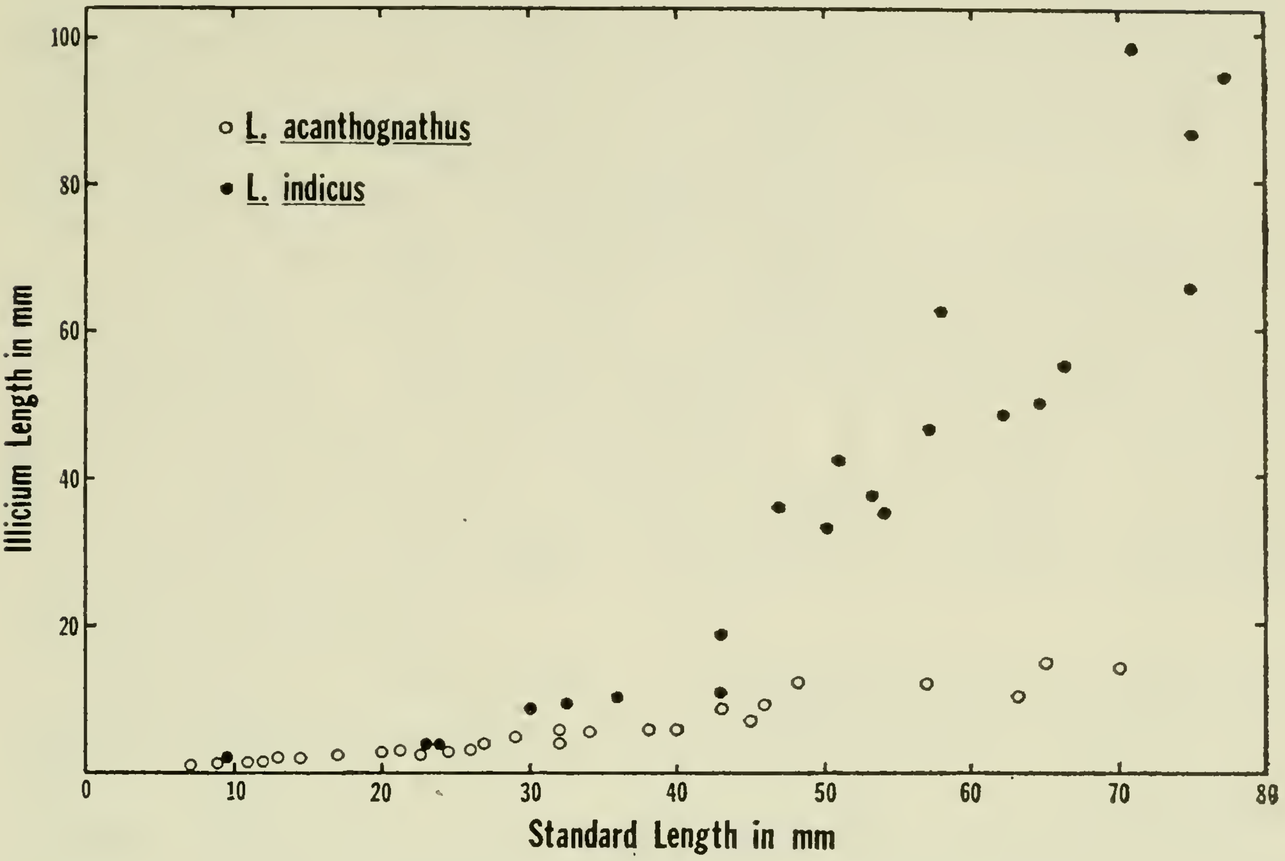

Figure 1. Relationship of illicial length and standard length for species of *Lophodolos.*

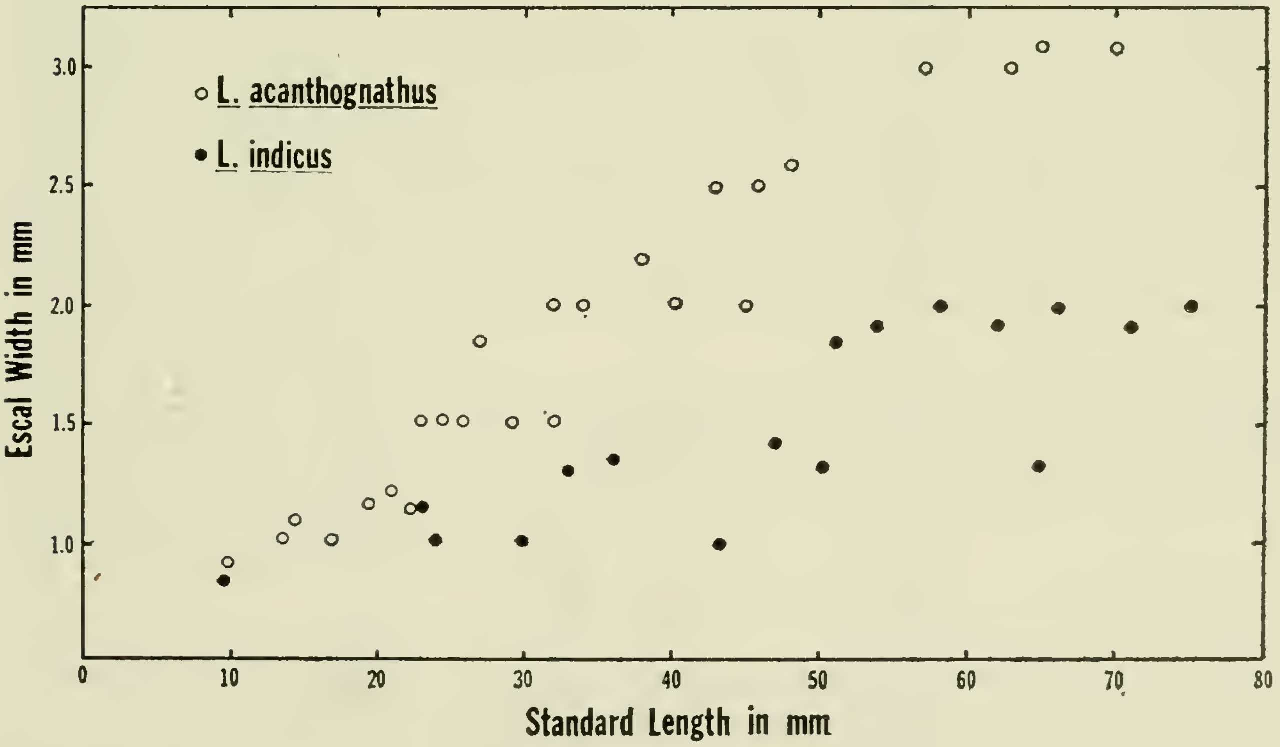

Figure 2. Relationship of escal bulb width and standard length for species of *Lophodolos.*

Table 1. Fin-ray frequencies for larvae and species of *Lophodolos*.

	Dorsal				Anal				Pectoral (left side)				
	5	6	7	8	4	5	6	7	17	18	19	20	21
Lophodolos sp. larvae[1]	1	4			2	3			1	2	1	1	
Lophodolos acanthognathus	5	17	1		2	20	1		3	8	5	3	
Lophodolos indicus		11	8	1		8	11	1	1	6	6	5	1
Total	6	32	9	1	4	31	12	1	5	16	12	9	1

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[1] Data from Bertelsen, 1951: 106.

Color in preservation dark brown to black over entire external surface of body except for bulb and appendages of esca (escal appendages and unpigmented distal portion of escal bulb silvery-white in unpreserved specimens of *L. acanthognathus;* E. Bertelsen, personal communication); oral cavity and guts except for outer surface of stomach wall unpigmented.

D. 5–8, first ray of dorsal fin reduced to a small stub; A. 4–7; P. 17–21 (Table 1); pelvics absent; C. 9 (2 unbranched – 4 branched – 3 unbranched); branchiostegal rays 6 (2+4).

Relationships. Lophodolos appears to be the most derived genus of the thirteen oneirodid genera. It is extremely specialized in many ways and, although probably derived from a *Microlophichthys*-like ancestor (a relatively primitive member of the family), it shows little resemblance to any other oneirodid (see Pietsch, 1974).

Distribution. Both species of *Lophodolos* have a wide horizontal distribution, and occur in all three major oceans of the world. *Lophodolos indicus* has not been taken in the western Atlantic where 82 percent of the material of *L. acanthognathus* has been collected. On the other hand, *L. acanthognathus* is represented in the eastern Pacific by only three specimens (Fig. 9).

Since virtually all collections of *Lophodolos* were made with nonclosing nets, vertical distributions are based on the maximum depths reached by fishing gear for each capture. Metamorphosed specimens were taken between approximately 650 m and an unknown lower limit. All specimens larger than 30 mm (37 individuals) were captured by nets fished below 1000 m; 62 percent of these were captured by nets fished below 1500 m. Material of both species from any one geographical area was insufficient to show whether there is any vertical separation between the two forms.

Comments. The original spelling of the generic name *Lophodolos* (Lloyd, 1909a), is reestablished as the "correct original spelling," as provided by Article 32(a) of the International Code of Zoological Nomenclature.

Key to the Females of the Species of the Genus Lophodolos

1A. Length of illicium less than 25 percent of SL in specimens 30 mm and larger (Fig. 1); width of escal bulb 4.4–6.7 percent of SL in specimens 25 mm and larger (Fig. 2); length of escal appendages 10.2–20.9 percent of SL in specimens 25 mm and larger, 8.7–22.2 (usually greater than 10.0) percent of SL in specimens less than 25 mm (Figs. 3–4); length of sphenotic spine 4.1–9.2 (usually greater than 6.0) percent of SL in specimens 30 mm and larger (Fig. 5); length of quadrate spine 2.9–6.5

(usually greater than 3.5) percent of SL in specimens 30 mm and larger (Fig. 6); D. 5–7 (Table 1) .... *L. acanthognathus* Regan, 1925.

1B. Length of illicium greater than 25 percent of SL in specimens 30 mm and larger (Fig. 1); width of escal bulb 2.1–4.0 percent of SL in specimens 25 mm and larger (Fig. 2); length of escal appendages 1.2–5.0 percent of SL in specimens 25 mm and larger, 4.2–10.5 (usually less than 9.0) percent of SL in specimens less than 25 mm (Figs. 3–4); length of sphenotic spine 1.9–6.0 (usually less than 5.0) percent of SL in specimens 30 mm and larger (Fig. 5); length of quadrate spine 1.6–5.0 (usually less than 3.0) percent of SL in specimens 30 mm and larger (Fig. 6); D. 6–8 (Table 1) .... *L. indicus* Lloyd, 1909a.

Lophodolos acanthognathus Regan, 1925

Figure 3

Oneirodes n. sp. Murray and Hjort, 1912: 104, fig. 90 (erroneous designation; specimen referred to *L. acanthognathus* by Nybelin, 1948).

Lophodolus acanthognathus Regan, 1925: 563 (original description; two specimens; lectotype designated by Bertelsen, 1951, ZMUC P92104, 12.0 mm; DANA Station 1358 (5), western North Atlantic, 28°15′N, 56°00′W; 3000 m wire; 1530 hr; 2 June 1922). Regan, 1926: 30, pl. 6, fig. 1 (brief description; one additional specimen). Regan and Trewavas, 1932: 83 (description after Regan, 1926; five additional specimens; *L. lyra* Beebe, 1932, a synonym of *L. acanthognathus*). Gregory, 1933: 402, 404, figs. 274, 276A, 277 (osteological comments; specific name misspelled *acanthagnathus* in fig. 277). Beebe, 1937: 207 (45 specimens listed from Bermuda). Nybelin, 1948: 86–89, Text-fig. 9, table 20 (*Oneirodes* n. sp. of Murray and Hjort, 1912, referred to *L. acanthognathus;* description of an additional specimen; comparison with previous descriptions; geographic, bathymetric distribution). Bertelsen, 1951: 107, figs. 64–65, tables 21–22 (synonymy; description; comparison with all known material; DANA material listed; comments; in key). Grey, 1955: 299 (one additional specimen). Grey, 1956: 255 (synonymy; vertical distribution).

Lophodolus lyra Beebe, 1932: 96–98, fig. 28 (original description; about 40 specimens; holotype, USNM 170949, 47.0 mm; GLADISFEN Net 111, 32°12′N, 64°36′W; 1463 m; 27 July 1931). Koefoed, 1944: 7, pl. 3, fig. 3 (misidentifications; description; three specimens including *Oneirodes* n. sp. of Murray and Hjort, 1912).

Lophodolos acanthognathus, Fowler, 1936: 1340, 1365, fig. 560 (corrected spelling; brief description after Regan, 1926). Pietsch, 1972a: 35, 45 (osteological comments). Pietsch, 1974: in press (osteology; relationships).

Material. Seventy-six female specimens, 6.0–70.0 mm: BMNH 4(18.0–26.0 mm); BOC 3; BZM 3(8.5–51.0 mm); FMNH 1(9.5 mm); GNM 1(56.0 mm); ISH 6(46.0–70.0

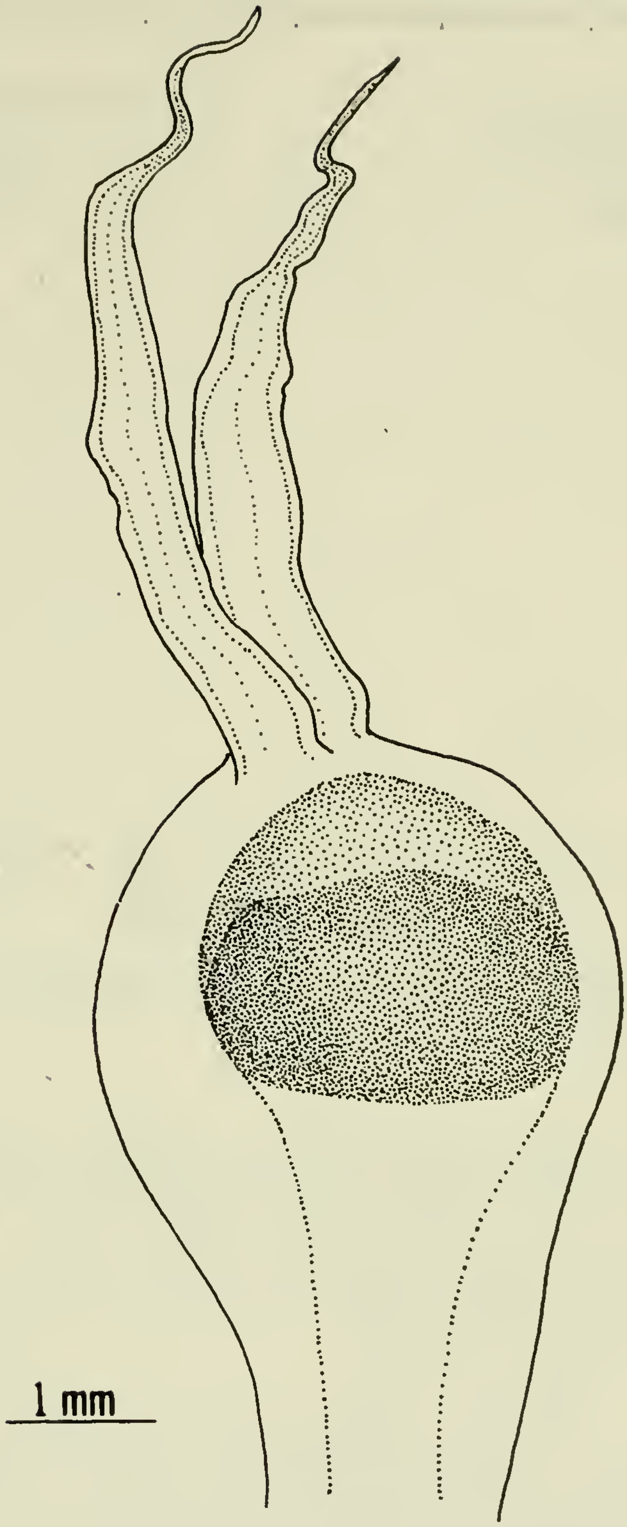

Figure 3. Esca of *Lophodolos acanthognathus,* LACM 10011-9, 38.0 mm, left lateral view. Drawn by Patricia Chaudhuri.

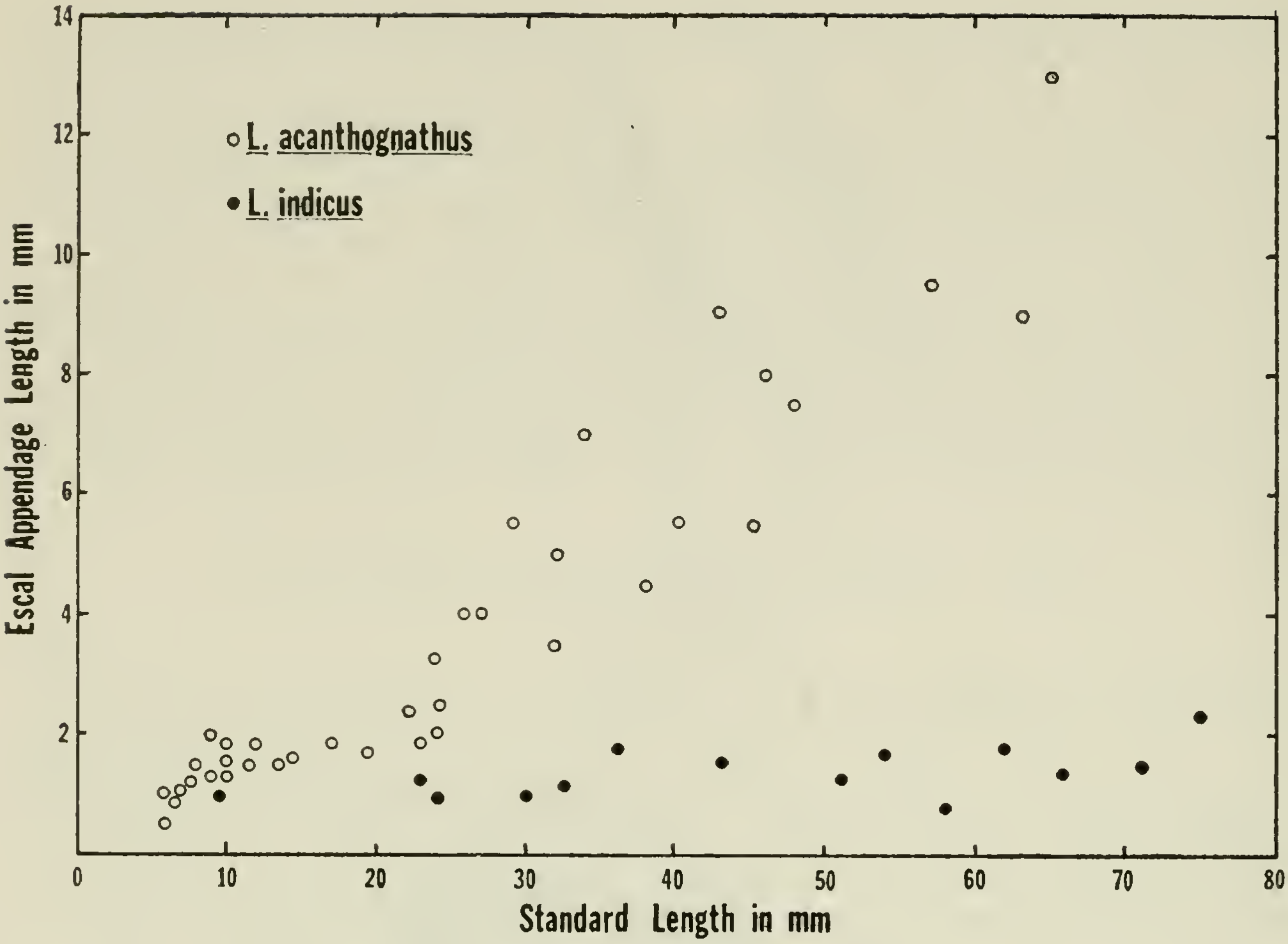

Figure 4. Relationship of escal appendage length and standard length for species of *Lophodolos.*

mm); LACM 4(22.5–38.0 mm); MCZ 2(18.0–65.0 mm); ROM 13(17.0–57.0 mm); SU 32(6.0–32.0 mm); USNM 2(10.0–47.0 mm); ZMUC 5(8.5–40.0 mm).

Diagnosis. See key to species.

Description. Illicium short, 11.1–23.1 (Fig. 1); width of escal bulb large, 4.2–9.0 (Fig. 2); escal appendages long, 8.7–22.2 (Figs. 3–4); sphenotic spines long, 4.1–9.2 (Fig. 5); quadrate spines long, 2.9–6.5 (Fig. 6); D. 5–7 (only one specimen had D. 7, ISH 500/73); A. 4–6; P. 17–21 (Table 1) (measurements in percent of SL; spine lengths based on specimens greater than 30 mm, fin ray counts on specimens greater than 20 mm).

Rest of characters as for genus.

Distribution. Lophodolos acanthognathus is known from both sides of the Atlantic. The vast majority of specimens (82 percent, including all type material) have been collected from the western half of this ocean as far east as 26°W, between 58°N and 25°N. In the eastern Atlantic the range extends from approximately 48°N, 18°W, southward, off the southern tip of

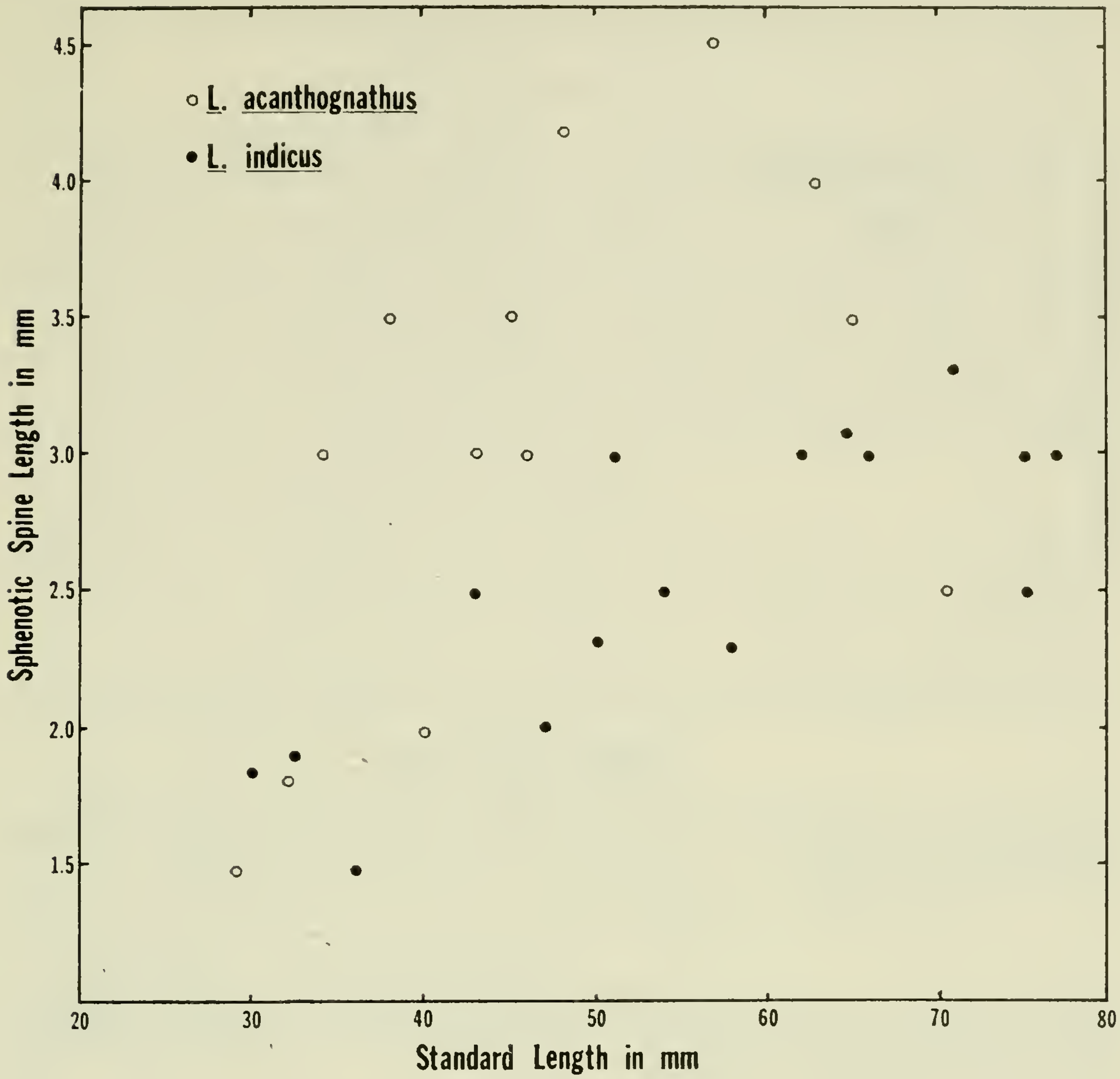

Figure 5. Relationship of sphenotic spine length and standard length for species of *Lophodolos*.

Portugal and the continental slope of Africa to 2°S, 26°W. A single record is known from the central South Atlantic at approximately 40°S, 26°W.

In the Indo-Pacific region *L. acanthognathus* is represented by three specimens: one from the Bay of Bengal, Indian Ocean (at approximately 7°N, 60°E), and two from the South China and Celebes seas. Three records are known from eastern Pacific Equatorial waters: on the equator at 139°W and from off the coast of Peru. The lectotype was collected from the western north Atlantic at 28°15′N, 56°00′W (Fig. 9).

On the basis of maximum depths reached by fishing gear, metamorphosed *L. acanthognathus* are vertically distributed between approximately 650 m and an unknown lower limit. All

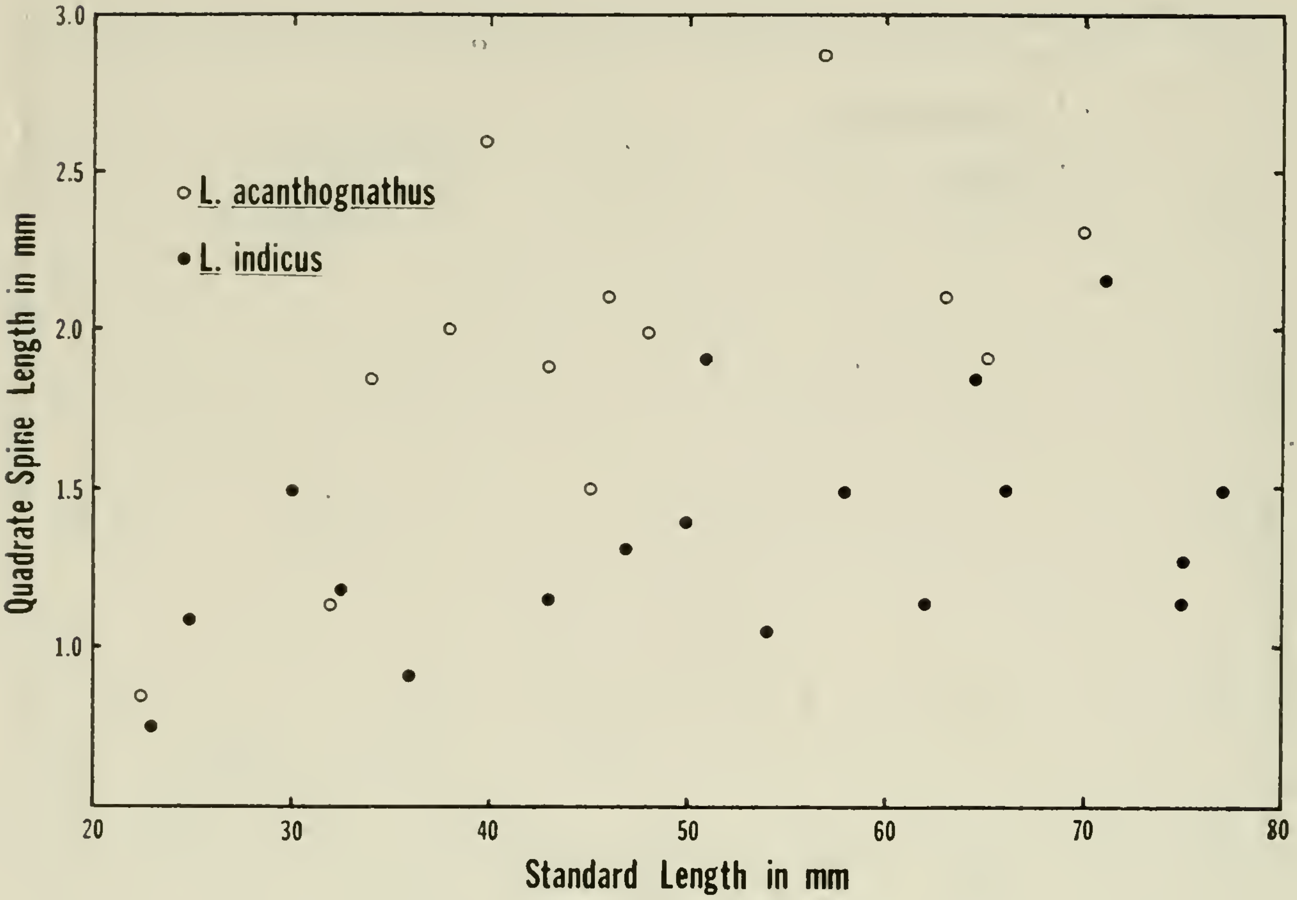

Figure 6. Relationship of quadrate spine length and standard length for species of *Lophodolos*.

specimens larger than 30 mm (19 individuals) were captured by nets fished below 1000 m; 58 percent of these were captured by nets fished below 1500 m.

Comments. Specimens of *L. acanthognathus* larger than approximately 30 mm can easily be separated from *L. indicus* on the basis of illicial and escal appendage lengths alone (see key to species). Smaller specimens, especially those less than 20 mm, are difficult to identify, and require a combination of meristics and counts, all of which overlap between the two species: illicial and escal appendage lengths, width of escal bulb, and dorsal fin ray counts (See Figs. 1–2, 4, Table 1). In some cases, geographic distribution may provide additional data for identification; *L. indicus* apparently does not occur in the western North Atlantic where approximately 82 percent (62 individuals) of the known material of *L. acanthognathus* has been collected (Fig. 9).

The holotype *L. lyra* Beebe (1932) compares well with the known material of *L. acanthognathus;* the name is retained as a synonym of *L. acanthognathus* following Regan and Trewavas (1932).

Lophodolos indicus Lloyd, 1909a

Figures 7–8

Lophodolos indicus Lloyd, 1909a: 167 (original description; single specimen; holotype, IMC 1024/1, 53.0 mm; INVESTIGATOR Station 307, off Kerala (formerly Travancore), southwest coast of India: 0–1624 m).

Lophodolus indicus, Lloyd, 1909a: pl. 45, fig. 7 (holotype figured). Regan, 1925: 563 (comparison with *L. acanthognathus*). Regan, 1926: 30 (brief description after Lloyd, 1909a; comparison with *L. acanthognathus*). Regan and Trewavas, 1932: 83 (after Lloyd, 1909a, Regan, 1926). Bertelsen, 1951: 108 (description after Lloyd, 1909a, Regan and Trewavas, 1932; comparison with all known material of *Lophodolos*). Grey, 1956: 255–256 (synonymy; vertical distribution).

Lophodolus dinema Regan and Trewavas, 1932: 83, pl. 4, fig. 3 (original description; single specimen; holotype, ZMUC P92105, 43.0 mm; DANA Station 3716 (2), South China Sea, 19°18′N, 120°13′E; 3000 m wire; bottom depth 3225 m; 1400 hr; 22 May 1929). Bertelsen, 1951: 108 (description; comparison with all known material of *Lophodolos*). Grey, 1956: 255 (synonymy; vertical distribution).

Material. Twenty-two female specimens, 9.5–77.0 mm: IMC 1(53.0 mm); ISH 5(36.0–75.0 mm); LACM 4(32.5–71.0 mm); MCZ 4(30.0–64.5 mm); NIO 1(57.0 mm); SIO 5(9.5–77.0 mm); UMML 1(23.0 mm); ZMUC 1(43.0 mm).

Diagnosis. See key to species.

Description. Illicium long, 15.2–138.0 (Fig. 1); width of escal bulb small, 2.1–5.2 (Fig. 2); escal appendages short, 1.2–10.5 (Figs. 4, 8); sphenotic spines short, 1.9–6.0 (Fig. 5); quadrate spines short, 1.6–5.0 (Fig. 6); D. 6–8; A. 5–7; P. 17–21 (Table 1) (measurements in percent of SL; spine lengths based on specimens greater than 30 mm, fin ray counts on specimens greater than 20 mm).

Rest of characters as for genus.

Distribution. In the Atlantic Ocean, *L. indicus* appears to be restricted to the eastern side; seven specimens are known from off the continental slope of Africa from 20°N, 21°W, east to the Gulf of Guinea and south to approximately 18°S, 10°W. The remaining material (15 specimens) is rather evenly distributed across the Indian and Pacific oceans between approximately 4°S and 30°N. The holotype was collected off the southwest coast of India (Fig. 9).

On the basis of maximum depths reached by fishing gear, metamorphosed *L. indicus* are vertically distributed between approximately 750 m and an unknown lower limit. All specimens larger than 30 mm (18 individuals) were captured by

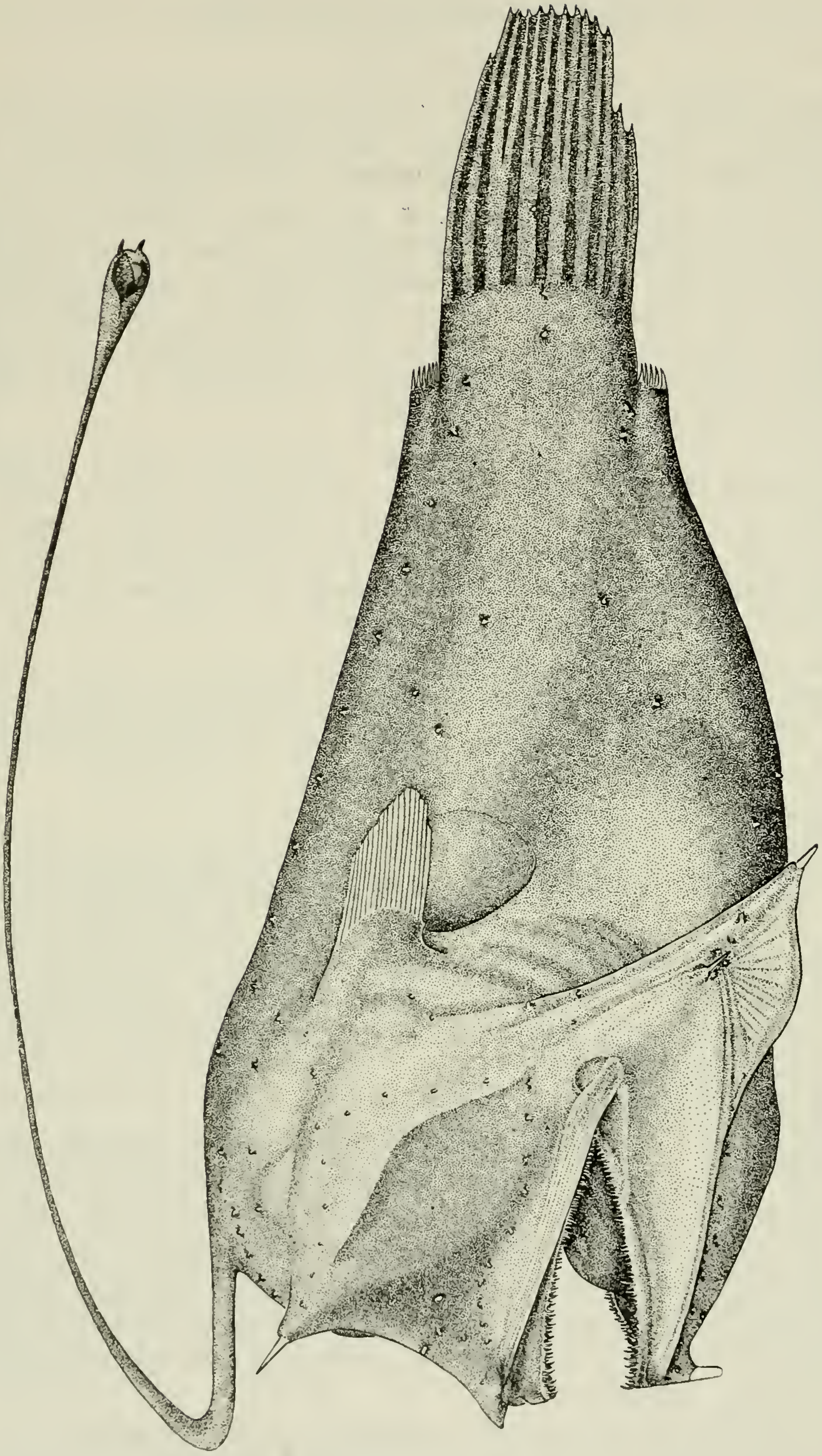

Figure 7. *Lophodolos indicus*, MCZ 47559, 58.0 mm. Drawn by Patricia Chaudhuri.

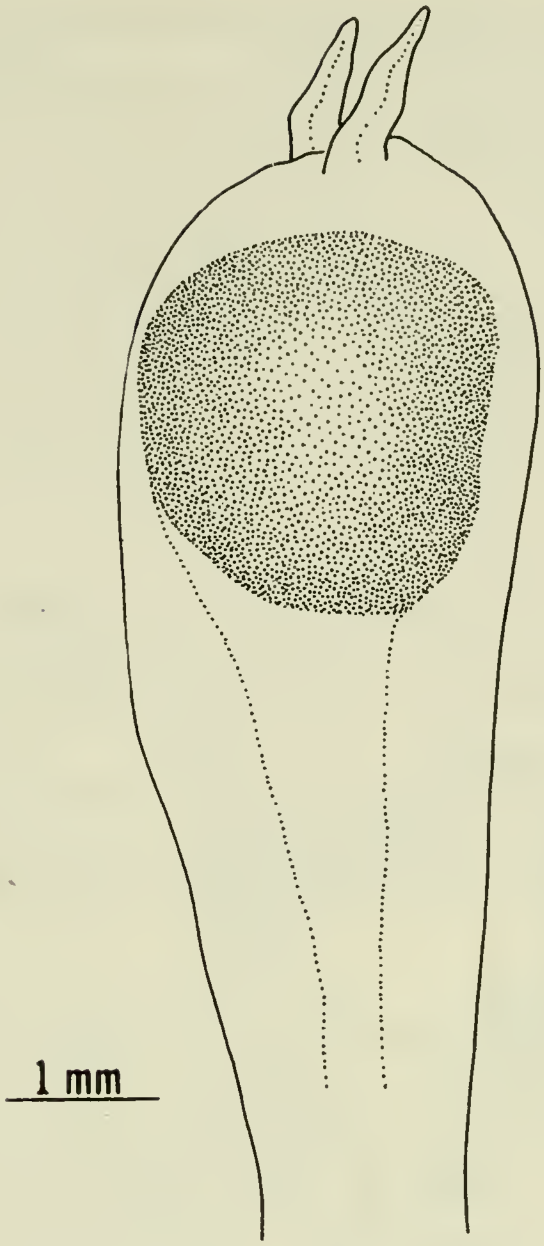

Figure 8. Esca of *Lophodolos indicus,* MCZ 47559, 58.0 mm, left lateral view. Drawn by Patricia Chaudhuri.

nets fished below 1000 m; 67 percent of these were captured by nets fished below 1500 m.

Comments. Large specimens of *L. indicus* (greater than approximately 30 mm) are easily distinguished from *L. acanthognathus* on the basis of illicial and escal appendage lengths alone (see key to species). Smaller specimens are more difficult to identify (see comments under *L. acanthognathus*).

Lophodolus dinema Regan and Trewavas (1932) was described as new on the basis of an escal morphology differing from that of *L. indicus.* These differences, however, are undoubtedly the result of damage. The esca of the holotype of *L. indicus,* originally described by Lloyd (1909a: 167) as being "hard but . . . covered with short, shreddy filaments," has lost

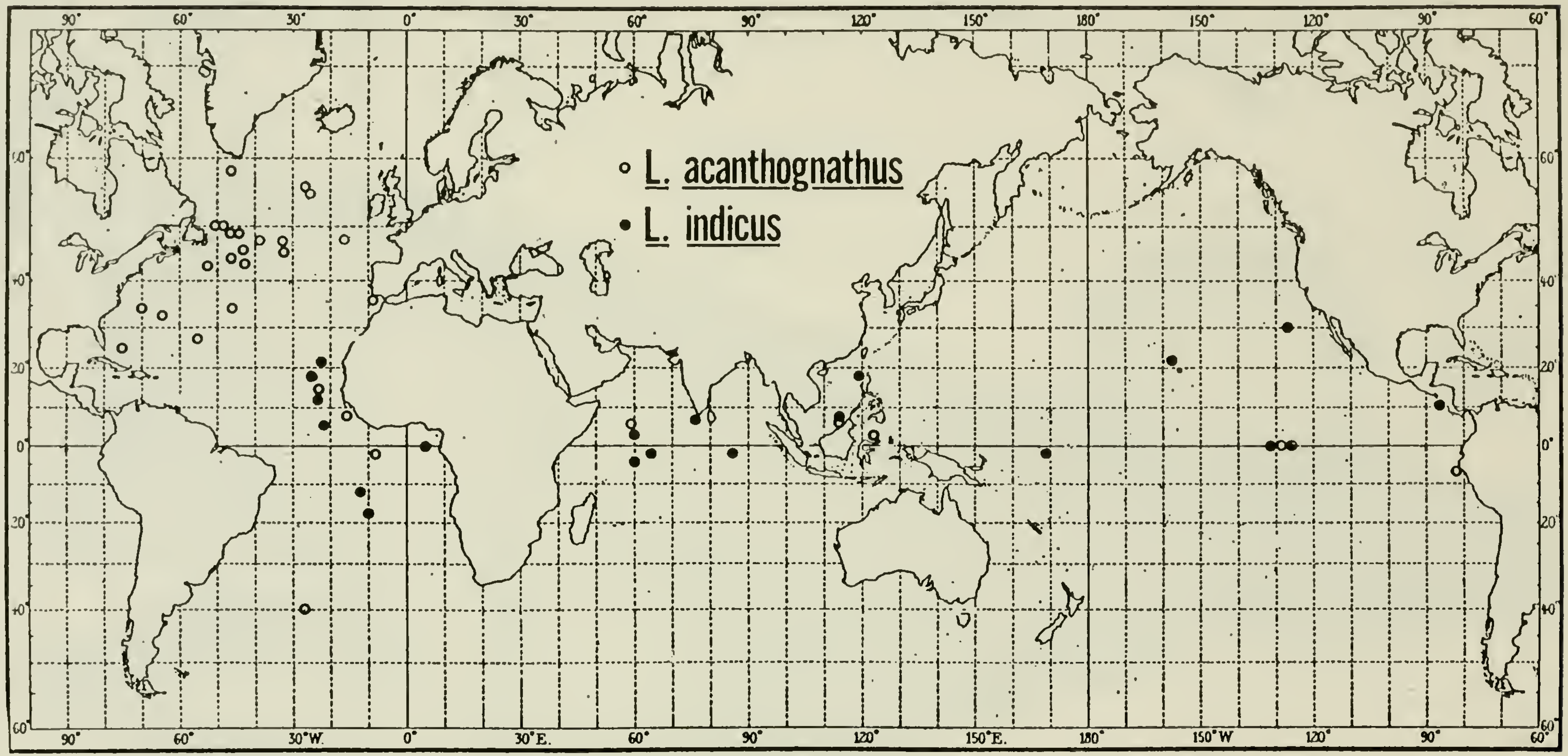
L. acanthognathus
L. indicus
90°
60°
30°W.
0°
30°E.
60°
90°
120°
150°E.
180°
150°W
120°
90°
60°
60°
40°
20°
0°
20°
40°
60°

Figure 9. Known geographical distribution of species of *Lophodolos*. A single symbol may represent more than one capture.

the two bilaterally placed appendages found in the holotype of *L. dinema* and in all known specimens of *Lophodolos.* Although I did not see it, the poor condition of the esca was confirmed by a sketch made from the holotype of *L. indicus* provided by A. G. K. Menon of the Zoological Survey of India. Discrepancies in illicial length (Bertelsen, 1951: 107) are also more apparent than real. A plot of illicial length against standard length (Fig. 1) shows the holotype of *L. dinema* to compare well with the material here considered to be *L. indicus.* In the absence of any significant differences, *L. dinema* is here synonymized with *L. indicus.*

Species Incertae Sedis

Lophodolos biflagellatus Koefoed, 1944, *nomen nudum.*

Lophodolus biflagellatus Koefoed, 1944: 7.

Comments. This name was used by Koefoed in a manuscript dated 1918 (not seen by me), and later mentioned in published form (Koefoed, 1944: 7) without application to a description or type.

SPECIES RELATIONSHIPS

Lophodolos acanthognathus and *L. indicus* are distinguished on the basis of five characters: illicial length, escal bulb width, escal appendage length, sphenotic spine length, and quadrate spine length. For most of these characters it is difficult, if not impossible, to know whether a character state represents a primitive or a derived condition. The longer illicium of *L. indicus* (Fig. 1), however, is surely a derived state; an increase in illicial length is a trend found within other oneirodid genera (*Dolopichthys, Oneirodes,* and *Chaenophryne;* Pietsch, 1972b, 1974). The width of the escal bulb of *L. acanthognathus* is like that of nearly all other oneirodids; the considerably narrower bulb of *L. indicus* (Fig. 2) is most likely a derived condition. *Lophodolos acanthognathus* has significantly longer escal appendages than *L. indicus* (Fig. 4), perhaps representing a derived state; longer escal appendages and filaments are found in the more derived species of *Oneirodes* (Pietsch, 1974). The sphenotic and quadrate spines of *L. acanthognathus* are long relative to those of *L. indicus;* either character state, long versus short, may represent the derived condition. From this character analysis, it is reasonable to speculate that *L. indicus* is the more derived member of the genus.

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ASSOCIATION OF *URSUS ARCTOS* AND *ARCTODUS SIMUS* (MAMMALIA: URSIDAE) IN THE LATE PLEISTOCENE OF WYOMING

Björn Kurtén[1] and Elaine Anderson[2]

Abstract. The first substantiated association of *Ursus arctos* and *Arctodus simus* (Mammalia: Ursidae) from a local fauna south of Alaska is reported from Little Box Elder Cave, a late Pleistocene site in Converse County, Wyoming. *Ursus arctos,* the grizzly or brown bear, entered the area from Alaska at the end of the Wisconsin glaciation, and may have been a factor in the extinction of *Arctodus simus,* the great short-faced bear.

INTRODUCTION

The late Pleistocene Carnivora of Little Box Elder Cave, Converse County, Wyoming, were described by Anderson (1968), who noted the presence of the grizzly or brown bear, *Ursus arctos* L. The material consists of a number of loose teeth and foot bones, most of which belong to a large form of this species. Extended comparison has shown, however, that at least one and probably two specimens must be referred to a distinct species and genus, the extinct short-faced bear, *Arctodus simus* (Cope). This is the first substantiated record of association between these two species of bears south of Alaska. The material is in the University of Colorado Museum (UCM), Boulder.

MATERIAL

Ursus arctos L., Brown bear

UCM 22289, right M_1. This tooth belonged to a young individual and shows hardly any trace of wear. The posterointernal part of the talonid has been lost. The remainder of the tooth is well preserved and is similar to the M_1 in Recent *U. arctos* from Alaska except for its somewhat larger size (Table 1). The lower carnassial of *Arctodus simus,* in possessing a powerful trenchant trigonid, differs markedly from the specimen at hand, and is also considerably larger, as shown in Table 1.

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UCM 49–40 and 22290, left and right M_2. As in No. 22289, these two teeth are quite unworn and probably belonged to the same individual. The left tooth is much damaged, while the right one is intact except for a missing piece of the protoconid, and the loss of the anterior root. This root, however, is preserved in the left M_2. As far as can be seen from the preservation, the two teeth are mirror images of each other.

The occlusal surface is strongly marked, with large, well-developed cusps delimited by furrows. Protoconid, metaconid and entoconid are all duplicated; the two cusps in a pair are subequal in size except for the protoconid, where the anterior cusp is noticeably bigger. The posterior rim of the tooth forms a small hypoconulid. A well-developed external cingulum curves around the hind edge of the tooth; there are no cingula in front or internally.

Despite its large size, approximating to the average in *A. simus,* M_2 has typical *U. arctos* characters. The second molar of *A. simus* differs in being narrow posteriorly, in lacking an external cingulum, and in having a markedly inward slope to its outer wall, as well as in various morphological details of the occlusal surface.

Although these M_2 are larger than those of present-day Alaskan *Ursus arctos,* late Pleistocene specimens of comparable size are known from Alaska (Table 2). An analogous decrease in size within *U. arctos* since late Pleistocene times has been documented in Europe (Kurtén, 1959, 1968).

USM No. 52–73, first phalanx, probably from the manus. The relatively small size of this bone, which has a length of 37 mm and measures 11.6 mm transversely in the middle, leads us to regard it as most probably being *U. arctos.* It agrees in size with those of present-day grizzly bears.

Arctodus simus (Cope), Short-faced bear

UCM 22288, left M^2. This tooth belonged to an old individual, and the four principal cusps have worn down to the same level as the cuspules. The anteroexternal corner of the tooth, the inner and outer roots, and some other portions of the crown have been lost; the anterior and posterior roots are preserved.

In spite of the damage, there can be no doubt about the characteristic outline of the *Arctodus* M^2. It is approximately triangular in shape, being broad in front and tapering rapidly posteriad; the inner wall is straight but the outer wall has a rounded bulge at the base of the metacone. In *Ursus arctos,* M^2 is a relatively longer and narrower tooth, and is not similarly tapered towards the hind end of the talon. The specimen matches closely the M^2 in specimens of *Arctodus simus* from Alaska with which it has been compared. Its size is close to the average for *A. simus* from Potter Creek Cave, California (Kurtén, 1967; see also Table 3).

UCM No. 7–56, left pisiform. The morphological characters and relatively slender build of this bone lead us to refer it to *A. simus.* It compares closely with the specimen from Rancho La Brea figured by Merriam and Stock (1925), and deviates in various respects from a specimen of *U. arctos* of comparable size; the last mentioned is conspicuously heavier in build, as shown by the measurements (Table 4). In No. 7–56, the shaft is slenderer and the distal boss much more flattened than in *U. arctos.* The size of the specimen is about the same as in *A. simus* from Rancho La Brea and Frankstown Cave (see Kurtén, 1967:35, Table 14).

DISCUSSION

The bear fossils were found at various levels and locations in the cave. As Anderson (1968) pointed out, there has been some reworking of the unconsolidated deposit by rodents, especially *Neotoma cinerea.* This probably accounts for the fact that the two brown bear M_2 lay at different levels. The age of the fauna as a whole is late Wisconsin.

As far as we know there is no other locality south of the Fairbanks District, Alaska, that shows an association between these two species. *Ursus arctos* has been reported from the Rancho La Brea tar pits, which have also yielded *A. simus,* but as shown by Kurtén (1960) the only specimen definitely referable to the former comes from the postglacial Pit 10, where the short-faced bear is not present. The ursine bear of the main Rancholabrean fauna is the black bear, *Ursus americanus* Pallas, of which a very large form was present in North America during the Wisconsin. Its large size has led to confusion with the grizzly bear.

We suggest that *U. arctos* entered western United States at the end of the Wisconsin glaciation, presumably through the corridor between the Cordilleran and Laurentide ice fields, from Alaska, which it had colonized some time earlier. Once it had penetrated south of the ice sheet it extended its range far beyond its limits in historical times, as shown by finds in eastern Canada and the United States (Guilday, 1968). The great short-faced bear may have become extinct either as a result of competition with *U. arctos* or because its prey became extinct, or for some other reason; but the exact date of its extinction cannot yet be stated.

ACKNOWLEDGEMENTS

We would like to thank Peter Robinson, University of Colorado Museum; Richard Tedford, American Museum of Natural History; and John L. Paradiso, Bird and Mammal Laboratories, National Museum of Natural History, for letting us examine specimens in their care. We are indebted to National Science Foundation Grant No. GB 31287 to Professor Bryan Patterson for aid in carrying out this and other work on North American Pleistocene mammals.

ABBREVIATIONS

The following abbreviations are used in the tables:

F:AM — Frick Collection, American Museum of Natural History, New York.
LBEC-UCM — Little Box Elder Cave, University of Colorado Museum, Boulder.
USNM — National Museum of Natural History, Washington, D. C.
M — Mean
N — Number in sample
O.R. — Observed Range
S.D. — Standard Deviation

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Table 1. Measurement of M_1 in *Ursus arctos* and *Arctodus simus*.

	N	O.R.	M	S.D.
Trigonid length				
U. arctos				
Recent, Alaska — USNM	40	14.3–17.0	15.90±0.09	0.60
LBEC UCM 22289	1	–	18.0	–
A. simus				
Pleistocene	18	21.8–26.1	23.01±0.33	1.42
Trigonid width				
U. arctos				
Recent, Alaska — USNM	40	8.2–11.1	9.94±0.11	0.68
LBEC UCM 22289	1	–	11.0	–
A. simus				
Pleistocene	20	14.1–16.8	15.50±0.16	0.73

Table 2. Measurements of M_2 in *Ursus arctos*.

	LBEC UCM 22290	Pleistocene, Alaska F:AM A-200-6671
Length	30.6	32.3
Anterior width	19.5	19.5
Posterior width	20.0	20.8

Table 3. Measurements of M^2 in *Arctodus simus* and *Ursus arctos*.

	N	O.R.	M	S.D.
Length				
A. simus				
Pleistocene	27	33.3–41.4	37.60±0.4	2.1
LBEC UCM 22288	1	–	35.5	–
U. arctos				
Pleistocene, Alaska	1	–	45.0	–
Anterior width				
A. simus				
Pleistocene	27	21.3–25.8	23.66±0.23	1.20
LBEC UCM 22288	1	–	ca. 22.5	–
U. arctos				
Pleistocene, Alaska	1	–	24.0	–

Table 4. Measurements of Pisiform Bone in *Arctodus simus* and *Ursus arctos.*

	A. simus LBEC UCM 7-56	*U. arctos* USNM 199252
Greatest length	56.0	54.0
Greatest proximal diameter	31.0	32.0
Distal boss, long diameter	34.3	30.7
Distal boss, short diameter	18.5	21.8
Least width of shaft	15.4	16.8

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THE STRATIGRAPHY OF THE PERMIAN WICHITA REDBEDS OF TEXAS[1]

Alfred Sherwood Romer[2]

Abstract. A description is given of the topography of the limestones and sandstones that form the formation boundaries between the six units comprising the continental redbeds of north central Texas; the results are presented in two maps.

The Early Permian redbeds of Texas, those of the Clear Fork, and even more notably those of the still earlier Wichita Group, are of major importance in the history of vertebrates. These are the oldest beds in which there is present an abundant fauna of continental type. In earlier, Carboniferous deposits of various areas have been found a very considerable number of amphibian types, and even, in the late Carboniferous, early reptiles. But almost without exception Carboniferous deposits containing tetrapod vertebrates represent coal-swamp conditions, and it is not until we reach the Texas Wichita redbeds at the beginning of Permian times that we find a truly continental fauna. Specimens, to the number of several thousands, representing scores of amphibian and early reptile types, have been collected in these beds for nearly a century. It is clear that these beds, with more than a thousand feet of deposits, represent a very considerable period of time during which a fair amount of evolutionary progress and faunal change took place. Farther to the south and southwest the Wichita beds are mainly marine in nature, with identifiable limestones, and there competent stratigraphic work has been done. But with the transition to continental beds to the north and east the limestones fade out, and almost nothing has been done in the past to sort out the sequence of formations in the redbeds portion of the Wichita.

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[1] This paper was in essentially completed form at the time of Professor Romer's death in November, 1973. Miss Nelda Wright kindly finished the task of preparing the manuscript and maps for publication. (Ed.)

[2] Museum of Comparative Zoology, Harvard University.

In default of work here by the geologists, I decided a number of years ago (1960) that although not a stratigrapher or proper geologist, I myself must attempt to work out the sequence of formations in the Wichita beds.

The task, at first, seemed almost hopeless. Except on the fringes of the area, limestones, to serve as formation boundaries, were almost nonexistent. Sandstones could be observed here and there, but it seemed probable that these were channel sandstones of limited extent. The one saving grace was that almost all of the area concerned was oil-bearing, and that in consequence thousands of well logs were available. In these logs, identifiable limestone markers of late Carboniferous age could be located. Assuming (hopefully) that deposition of sediments was fairly uniform over the area concerned, it would be possible to lay out a sequence of formations by calculating the distance to the surface from such limestones and thus plot out a rough stratigraphic sequence.

A further discouragement lay in the fact that for almost all of the area no topographic maps were available. Apart from highway maps and blueprint land-ownership maps of the counties concerned (drawn up for the benefit of oil lease men), the only sources available were Department of Agriculture air photos, which show streams, hills and roads, but do not, of course, give any indications of elevation.

All in all, the prospect was most discouraging. But as I began work, I found that both nature and man rendered valuable aid. (1) As I said above, surface markers to distinguish formation boundaries appeared to be lacking. This proved, however, not to be the case. Upon study of the sandstones encountered, many of them proved to be wide ranging, and could be followed for a considerable distance cross country. Further, in most cases limestones that, to the southwest, were used as formation boundary markers, were found to change gradually to the northeast into sandy limestones, then into "limey" sandstones and straight sandstones, which could be traced across the entire area concerned.[1]

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[1] Had I read more carefully Cummins' last paper (1897) on the Wichita-Albany problem, I would have seen my discovery of this condition to have been anticipated by him. He states: "We found that a limestone in the Albany Division . . . gradually changed in composition to a calcareous sandy clay. . . . other limestone beds in the Albany division when traced to the northeastward would gradually pass into sandstone."

(2) Major aid came from another source. As noted above, almost no topographic maps of the area were available when I began to work. At about this time, however, an arrangement was made between the Texas Water Development Board and the Topographic Branch of the U. S. Geological Survey, to map a larger area, including almost every bit of the Wichita redbeds region, on a scale of 1:24,000. The work proceeded rapidly and presently proofs and finally finished sheets of the whole area became available. These were of inestimable value to me — most notably in giving accurate elevations (doing elevations by aneroid in the highly variable weather conditions of the Texas prairies is most unsatisfactory).

(3) A final aid in this work came as a result of the decision of the Texas Bureau of Economic Geology to prepare a geological map of the State, at a scale of 1:250,000, under the direction of Virgil Barnes. One of the first sheeets attempted was the Sherman Sheet, along the north border of the State. The Cretaceous covers most of the territory, but much of the western margin, in Montague County, lay in the Permian. Almost no definite formation markers were available in this area, but it was found (as I had found) that certain sandstone beds could be traced for a considerable distance. These were followed out by J. H. McGowen westward across Montague County and into Clay County to the west. These sandstones were merely given numbers on the published Sherman Sheet; I found, however, that certain of them were identical with formation boundaries that I had been following eastward. In almost every instance, McGowen's findings and mine coincided. It was a pleasure to have my work independently confirmed and, in fact, in a few areas in Clay and Montague Counties, I saved my weary feet and accepted McGowen's findings in completing my course over to the Cretaceous boundary.

I owe thanks to a very considerable number of people and institutions for aid during the course of this work. Notably, I am deeply indebted to my wife, Ruth Hibbard Romer, who accompanied me on almost all of my trips to the area, furnished my transportation and day after day picked me up, footsore and weary, after a long trek across the cow pastures. John Kay, consulting geologist of Wichita Falls, who is an authority on the geology of the Wichita region, aided throughout with encouragement, advice, and specific data. The Gulf and Humble Oil companies gave me access to their well log collections and to unpublished maps, surface and subsurface, and the first-named company presented me with a large collection of duplicate well logs. Robert Roth of Wichita Falls gave useful advice in Wichita stratigraphy. Robert Craig, oil geologist of Olney, gave me the use of a very valuable series of well logs of Young County. I am indebted to Frank Gouin, oil geologist of Duncan, Oklahoma, for interesting discussions of the Montague County beds. Virgil Barnes aided greatly by making available to me McGowen's tracings. Adolph H. Witte of Clay County, who has done much work in archaeology and paleontology, gave much helpful advice. The maps here published were drawn by Carol Jones.

I cannot refrain from mentioning the late Fred B. Plummer, of the University of Texas and the Bureau of Economic Geology, who first interested me in the stratigraphy of these beds and who, had he not died at an unseemly early age, would have been deeply interested in the present work.

It is impossible in a short space to give thanks to the many landowners who have allowed me to wander over their pastures. My wife and I are most especially indebted to Mr. and Mrs. G. F. Boone and L. D. Boone of Godwin Creek, whom we have long cherished as valued friends, to James R. Parkey who has given us ready access to various areas that he owns in the Little Wichita country, and John Robinson of Archer City, ever hospitable to "bone hunters."

I am much indebted to the National Science Foundation for support of part of my earlier Texas work, for support of a final trip to the Texas beds in 1973, and for publication of this paper.

WICHITA STRATIGRAPHY

The first student of the Wichita beds was W. F. Cummins. Originally a frontier preacher, he was engaged by Cope to collect fossil vertebrates in the Texas redbeds, then turned geologist, served on the Texas Geological Survey during the few years of its existence, and later became geologist for the Southern Pacific Railroad. In his early work for the Texas Survey, Cummins (1891) believed conditions to differ north and south of the Brazos River. He established a Cisco Division as forming the uppermost section of the Carboniferous in the northern area. Included in the Cisco were the coal beds (which he lumped at that time as "Coal number 7" and, as seen on his plate VII, considered the top of the Cisco to lie not far above this coal). The typical coals of this area are contained in the Harpersville

Formation of most writers. In the northern region he believed the Cisco to be directly overlain by the Wichita beds, which thus, as later identified, begin with the Pueblo Formation (in which are found the lowest redbeds in southeastern Archer County). In this northern area he believed the top of the Wichita beds to lie at a double limestone seen along the Big Wichita River a few miles west of the Archer-Baylor county line (1891: 402). This limestone is clearly the Bead Mountain Limestone, forming the boundary between Belle Plains and Clyde formations. Cummins' original Wichita thus included, in ascending order, the Pueblo-Moran-Putnam-Admiral-Belle Plains formations of later terminology; the Clyde Formation, later considered an integral part of the Wichita, was in this discussion thought to be a lower element of the Clear Fork.

Farther south, beyond the Brazos in Young and Stephens, Throckmorton and Shackleford counties, Cummins found a different situation. Above the Cisco are formations that are mainly marine in nature, which he did not realize were identical with his Wichita beds to the north. He believed these beds, which he termed the Albany Division, to be a terminal part of the Carboniferous intercalated between the Cisco and the Permian redbeds. The upper boundary of the Albany beds (1891: 404) he believed to lie between California Creek and the Clear Fork, about on the Shackelford-Haskell County boundary. He thus considered the Lueders as the top of his Albany beds, above which lay the Clear Fork redbeds.

Two years later (1893, especially p. 223) Cummins began to suspect that his Albany beds were merely a different facies of the Wichita beds. And in 1897 he confirms this suspicion, and definitely traces certain "Albany" beds northward into the "Wichita" region with a transformation of their character from marine to continental in nature. As a result, the term "Albany" was abandoned and the pre-Clear Fork Permian beds were termed Wichita — although some confusion remained as to boundaries between Cisco and Wichita and between Wichita and Clear Fork.

For many years little was added to our knowledge of these beds. Adams (1903) and Gordon (1911 (with others), 1913) confirmed Cummins' identification of the Wichita and Albany, and Gordon reasonably concluded that in the northern area the beds from the Bead Mountain Limestone to Lueders should be included in the Wichita.

A landmark in the history of the group was the publication in 1922 of "Stratigraphy of the Pennsylvanian Formations of North-Central Texas" by F. B. Plummer and R. C. Moore. While their attention was centered on the late Carboniferous, the Wichita formations were discussed as well. The beds which Cummins considered to constitute his Cisco division were divided, in ascending order, into the Graham, Thrifty, and Harpersville formations (the last including the coal beds). Cummins considered all higher beds as part of his Wichita. But since at the time of publication of Plummer and Moore's paper the Carboniferous-Permian boundary was believed to be at a considerably higher level, three further formations — Pueblo, Moran, and Putnam — were included by them in the Cisco, and only the formations lying above the Coleman Junction Limestone at the top of the Putnam Formation — Admiral, Belle Plains, and Clyde formations and, finally the Lueders Limestone — were considered to constitute the Wichita Group.

Subsequent to the publication of Plummer and Moore's basic work, the stratigraphy of the Cisco and Wichita has been discussed by a number of workers. For example, Sellards, in the comprehensive "Geology of Texas" (1933), follows in general Plummer and Moore, but since by that time it was generally agreed that the Carboniferous-Permian boundary had been placed too high in the section, the Moran and Putnam formations were included in the Wichita Group. In 1940, M. G. Cheney, oil geologist and an able student of Texas geology, proposed a radical change in treatment. Former "groups" became "series"; the former formations became "groups" and were subdivided into rather thin formations. During the years preceding this publication the invertebrate paleontologists had established a sequence of marine Permian beds in West Texas, termed the Wolfcamp and Leonard Series, the base of the Wolfcamp being considered the base of the Permian. Cheney proposed abandoning the established terms "Wichita" and "Clear Fork" and substituting the West Texas local terminology. The evidence of foraminifera indicates that the base of the Wolfcamp can be equated with a point in the Waldrip shales, somewhat below the top of Harpersville. Cheney solves this problem by abolishing the Harpersville "series," the top levels being included in the Pueblo, and the rest of the Harpersville being lumped with the Thrifty. The foraminiferal evidence indicates equivalence of the top of the Wolfcamp with about the middle Admiral. Cheney hence reduced the Admiral by half, adding the upper part of the formation to the Belle Plains.

Moore returned to the Texas redbeds region in 1949 with the study of the geology of the Permian in the Colorado River region. He followed Cheney in part, by including the upper part of the Harpersville in the Pueblo, and including the upper part of the Admiral in the Belle Plains. However, he refused to raise the "formations" to "series" level. Furthermore, he retained the term "Wichita Group" for formations from the Pueblo Formation (expanded) to and including the Lueders, but parallels Cheney in also noting "beds of Wolfcamp age" and "beds of Leonard (?) age" at the levels given by Cheney.

In this present attempt at interpreting the stratigraphy of the Wichita beds, I have essentially followed Plummer and Moore. The finer subdivisions proposed by Cheney may be followed in the marine section, but are impossible to sleuth out in the continental beds. Nor can the subdivision proposed by him within the Harpersville and Admiral formations be readily followed in the continental areas with which we are concerned. I have adopted the base of the Pueblo as the base of the Wichita. This is in accord with Cummins' original definition of the Wichita, since the actual base of the redbeds type of deposit is at the base of the Pueblo Formation. Although I am far from certain that the base of the Wolfcamp of West Texas has any necessary relation to the true Carboniferous-Permian boundary, this equivalent is but slightly below the base of the Pueblo. It is generally overlooked by invertebrate paleontologists that, considering that the extent of the Permian was for a long time (and still is) a rather vague and ill-defined matter, the real point in question is not the base of the Permian but the top of the Carboniferous, a matter for settlement by paleobotanists. But both invertebrate and botanical evidence agree that the Permian base is a short distance below the base of the Pueblo, and since this exact point cannot be accurately determined in the continental beds, the slightly higher Saddle Creek Limestone, which can be readily followed, seems a satisfactory point for Cisco-Wichita division.

Methods. The results of my field work are shown on the three accompanying maps, on which I have attempted to exhibit the subdivision of the beds into six successive formations, from the underlying Cisco beds of the Carboniferous up to the Clyde Formation and the Lueders Limestones, which cap the Wichita and form the boundary with the overlying Clear Fork. The formation boundaries, as traced, were at first entered on the air photographs, later on the 1:24,000 topographic sheets. It is, of course, impractical to publish them on this scale. Maps 2 and 3 are executed on a two-miles-to-the-inch scale, which will, I think, be sufficient for future workers to locate the horizon of their finds with reasonable accuracy.

The method followed was to pick up each successive limestone used as a formation boundary where already known and mapped, in the southwestern part of the region, and then follow it northward and eastward cross-country as it changed toward and to the condition of a sandstone. In some areas a continuous tracing was possible. Over much of the region, however, the rolling prairie surface makes this impossible, and I have had to seek out occasional small outcrops or detached slabs in the pasture grass, much in the fashion of a "paper chase." Under such conditions, of course, it was possible to stray from one sandstone to another, above or below. But over most of the territory there exists such a profusion of well logs that a check on elevations above the underlying limestones of the Cisco Group was present as a corrective.

All the stratigraphic studies mentioned earlier have been made in the region to the south of the true redbeds area; almost no previous attempts at stratigraphic subdivisions of the continental beds have been made. The sole exception was that in the 1920's, a time at which it was believed that the Coleman Junction Limestone represented the Carboniferous-Permian bondary, a reconnaissance was made of the probable course of this horizon from the point at which the limestone disappears in southwest Archer County north and east to the Red River (Timms, 1928). Some years ago (1958) in a general essay on the redbeds and their fauna I included a rough sketch of the probable formation boundaries in the redbeds area.

The general area to be considered is bounded on the north by the Red River; to the west by the Clear Fork beds above the Lueders Limestone, running north to south through Wilbarger, Baylor and Throckmorton counties. To the east, in Montague County, the Wichita beds disappear beneath the Cretaceous deposits. To the south we reach the base of the Wichita beds along a line somewhat south of the Jack County boundary. To the southwest the formations of the Wichita Group continue, but gradually change from continental to marine beds — that is, from "Wichita" type beds to sediments of "Albany" nature. South of the Brazos River vertebrate fossils become scarce, and very few have been found in the Wichita beds beyond the southern boundary of Throckmorton County.

The geologic structure of the area is a simple one. The area is in general a northern continuation of the Bend arch. In eastern Young County and northward the beds dip to the north; west of this line, the dip is to the northwest (Hubbard and Thompson, 1926). In the southern part of the region the dip is on the order of 40–50 feet to the mile. Farther north the dip decreases, and in the upper beds, found on the surface toward the Red River, the beds are nearly horizontal. Near the river, the deeper beds in certain areas have been strongly affected by the east-west Electra arch and, farther east, by the Muenster arch. Arch activity, however, appears to have ceased before deposition of the surface beds here, and in general, these structures have had no effect on the surface stratigraphy. To the east, in southern Montague County we encounter the margin of the Fort Worth basin, with strong dips to the east and northeast in the lower beds.

One tends to think of the change in the nature of the Wichita beds as being a north-to-south shift from continental to marine. Actually it seems that it is an east-to-west transition. The general redbeds area appears to have been a lowland, with (presumably) high land to the east and a sea to the west. As is known from well logs, the Wichita redbeds formations became mainly marine west of a line extending from central Wilbarger County south through central Baylor and Throckmorton counties. In the eastern parts of these counties there are occasional persistent limestones, but redbeds tend to dominate and almost no limestones persist east of the east line of these counties.

As an aid to future workers who wish to check — or correct — my findings, I herewith add some detail as to the nature of my work on the various formation boundaries.

The Saddle Creek Limestone

As noted above, I consider the Pueblo Formation to be the basal member of the Wichita group; and I consider the Saddle Creek Limestone, at the top of the Harpersville, as furnishing a close approximation to the Carboniferous-Permian boundary.

The Saddle Creek Limestone is well developed in the more marine sections of the Wichita to the south, and can be followed north as far as the Clear Fork of the Brazos, not far south of the Young County line. It can be traced into southwestern Young County only with difficulty and with doubt. Plummer and Moore identify it for a distance west of the Salt Fork southwest of Newcastle, but it is probable that this is the somewhat lower Belknap Limestone, as is also presumably the case of the supposed Saddle Creek in this area marked on the 1937 Cooperative geological map (Plummer and Fuqua, 1937). Lee and colleagues (1938; cf. Cheney, 1940: 91 and fig. 10) figure the Saddle Creek, although with some doubt, at the head of Ratliff Branch in southwestern Young County. Here the limestone, feebly developed, is part of a thick sandstone layer that can be readily followed to the north and east across Young County, where it lies in proper relation to the underlying limestones in the Harpersville.[1] From the point mentioned above, the sandstone beds here accepted as the Saddle Creek equivalent turn westward along the south margin of the valley of Gibbens Creek, cross that creek and run northeastward along the north side of this valley to reach a prominent bluff close to the Brazos and directly west of Fort Belknap. The Saddle Creek Limestone then turns west, and becoming less well marked, descends down the west side of the valley of Postoak Creek and reaches a bluff south of the Salt Fork at the mouth of Elm Creek. It continues west south of Elm Creek, to disappear into the Salt Fork alluvium about a mile east of Proffitt. The Saddle Creek reappears on the north bank, only obscurely west of the mouth of Paint Creek (California Creek), but east of that creek capping Deer Head Bluff north of the Salt Fork bottoms. East of this bluff it turns northward west of Big Skid Creek and can be traced with some difficulty eastward across the flat country at the head of this creek and then southward along a low ridge west of Peveler Creek. Returning northward to cross this last creek, the outcrop continues eastward along the hills north of Newcastle to a prominent point about four miles northeast of Newcastle and a mile west of Salt Creek. From this point a series of outliers extends northeastward toward Jean, but the main outcrop turns northward along the west margin of the Salt Creek valley, descending to cross this creek a mile northeast of True cemetery. The outcrop turns southeastward for two miles, swings northward to cross Little Salt Creek, then southward and again northward to obscurely circumnavigate a flat area east of Jean. The outcrop turns south for about three miles, then north for six miles to Farmer, at a level of about 1150 feet, mainly following the base of the hills west of the road leading from State Highway 199 north to Farmer.

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[1] Galloway, in an interesting study of the Harpersville in subsurface (Galloway and Brown, 1972), gives a surface map on which the assumed Saddle Creek Limestone is shown for several areas in Young and Jack counties. Different areas indicated on this map, however, show the supposed Saddle Creek at several different levels, ranging from that of my assumed Saddle Creek up to that of the Camp Colorado, nearly 200 feet higher.

Southeast of this area, the country rises to the Loving region. My well records for this area are sparse, but it seems probable that there were several outliers of the Saddle Creek in this area, the principal ones being at the Loving settlement and along a ridge running eastward toward the county line. Galloway (Galloway and Brown, 1972) considers these beds to lie within the underlying Harpersville Formation, presumably because he generally places the Saddle Creek member at a higher level stratigraphically than I do.

From Farmer the main outcrop runs eastward two miles along a ridge between two tributaries of Brushy Creek, then westward south of these tributaries to a point north of Farmer. North of this tributary it runs eastward along a ridge, which becomes prominently developed, for about three miles, with outliers on Rattlesnake Mountain and Bare Mountain, and then turns northward, only to turn westward up a further northern branch of Brushy Creek. After crossing this branch near its head, the Saddle Creek comes east again several miles to Spy Knob. Thence the outcrop runs for some miles northwest, then northeast, then southeast, in so doing outlining a semicircle around the margins of the Prideaux structure (highly important in the days of shallow oil production). After crossing the Windthorst-Loving highway, the Saddle Creek outcrop (now in southeastern Archer County) runs eastward along the southern margin of a ridge for several miles, almost reaching the West Fork of the Trinity River. It then returns westward north of this ridge and then turns north and northwest, to subside to the level of the West Fork near its crossing by the Windthorst-Loving road, at about 1,000 feet.

We are now entering a wild region, where the West Fork and its tributaries have cut deep valleys, capped by sandstones and covered by scrub oak and tangles of vines, making a very complicated pattern. As noted below, the main outcrop of the Saddle

Creek extends eastward north of the West Fork along a general line south of the north border of Jack County, with a general elevation of about 1,000 feet close to the county boundary, but somewhat higher farther south. To the south, beyond the West Fork, are large areas of hills and plateaus, sandstone capped, which lie at higher levels, and which, by such well-log evidence as is available to me, indicate them to be extensive outliers of the Saddle Creek.[1] The most westerly of major outliers of this sort is one whose southwestern extremity is at Markley and extends northeast about five miles to a point south of the mouth of Brushy Creek and runs eastward a similar distance along the north side of Plum Creek. Much larger is a tableland that occupies the area between the valleys of Plum Creek and Cameron Creek and extends from three to five miles south of the West Fork and includes an area of 20 square miles or so. Farther east a smaller outlier lies between Cameron Creek and Roberts Prairie Branch and a final, still smaller, outlier is found east of this branch. Farther southeast, it is probable that the top of the Indian Hills attains the Saddle Creek level.

After crossing the West Fork, the main outcrop of the Saddle Creek, as noted above, runs eastward, roughly parallel to the Jack-Clay county boundary and some miles to the south. For the first mile or so below the crossing there is little evidence of the presence of the Saddle Creek in the alluvial river bottom, but east of the Jack County line it is visible as a sandstone low down toward the river level. Its eastward course is a zig-zag one, the outcrop running to the north up successive creek valleys and rising southward to bluffs north of the West Fork. A mile east of the Antelope-Jacksboro highway it extends a mile to the north up the valley of Flat Creek, where its elevation drops somewhat below 1,000 feet, and then returns southward to a river bluff at 1,040 feet — an elevation that matches that of the outlier south of the river. Four miles east of the highway crossing, it runs north a short distance in a valley in the Mount Lebo region, then returns south to cap a high river bluff at about 1,050 feet. A mile further east lies Lodge Creek, a major northern tributary of the West Fork; the outcrop extends north up this valley to well toward the county line southwest of Shannon, dropping below the 1,000-foot level in elevation. East of this creek the West Fork tends to swing to the southeast, and the main outcrop, continuing eastward, tends to leave the river, although east of Lodge Creek outliers form bluffs at about 1,050 to 1,080 feet. The Saddle Creek again extends well to the north up Turkey Creek, next to the east, but beyond this creek the outcrop turns eastward around the margins of the creek valley, sending, however, a high ridge southward and then westward to reach an elevation close to 1,100 feet. Next to the east is Jones Creek, which the Saddle Creek ascends to Postoak settlement. East of Postoak the Saddle Creek extends southward several miles along a high but narrow ridge, bifurcate distally, with an elevation now over 1,100 feet. East of this ridge the Saddle Creek runs northward up the north fork of Crooked Creek, to end in a "flat" about two miles in circumference, where there are few exposures except in road margins. Descending this creek branch, it runs about two miles east to ascend the east branch of Crooked Creek to a deep valley north of Galliher Mountain. East of this branch it runs southeast and east for about four miles along the summit of gentle slopes, past Truce church, rising as it goes, to reach a ridge at the southwest corner of Montague County at an elevation of about 1,150 feet. It then turns northward along a bluff for somewhat over two miles, losing altitude, to enter the southeast corner of Clay County at about 1,090 feet. There are certainly outliers to the northeast of this bluff, and I have mapped sandstone ledges here that are probably Saddle Creek equivalents. From the southeast corner of Clay County the Saddle Creek turns westward along the foot of the hills south of Newport.

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[1] Galloway (Galloway and Brown, 1972) believes these sandstones to lie within the Harpersville; but this belief is due to the fact that the outcrop to the north, which he indicates as the Saddle Creek, is quite surely the Camp Colorado, nearly 200 feet higher in the section.

From this point eastward my subsurface data are not sufficient for me to be certain of the position of the Saddle Creek. There is certainly a sharp dip to the northeast, where we are entering the Fort Worth basin. It appears to be represented in hills north and northeast of Newport along the course of Big Sandy Creek toward and to the Montague County line and on northeast to Prairie Branch. Crossing this branch it appears to be continued by sandstones following the north shores of Lake Amon G. Carter, and then following for some distance up the valleys of Jones Creek and East Jones Creek, disappears under the Cretaceous about four miles south of Bowie.

CAMP COLORADO LIMESTONE

The uppermost member of the Pueblo Formation is the Camp Colorado Limestone, which separates the Pueblo from the Moran Formation. It has long been known farther south, and is rather incompletely shown on the southwestern part of the geological map of Young County (Plummer and Fuqua, 1937), running north close to the Throckmorton County line northward toward Elm Creek. From west of Murray in southwestern Young County, it runs northward about three miles along the west edge of the Fish Creek drainage area, then turns back southwest for two miles east of Dry Branch of Elm Creek, then traces northward west of Dry Branch on one side or the other of the county line. It follows the west side of Dry Branch almost to Elm Creek, ending this course in a prominent bluff. It then turns back south along gentle slopes east of Meyers Branch, which it crosses about two miles south of Elm Creek. The Camp Colorado is not exposed along its course down the west side of Meyers Branch except at the foot of the bluff west of the branch close to Elm Creek. A mile west of this point the Camp Colorado can be seen at the bottom of the channels of Elm Creek and its tributary Bush Knob Creek.

North of Elm Creek slopes are gentle, but occasional traces of the Camp Colorado can be made out as it runs northeastward, gaining slowly in elevation and for some distance lying close to the state highway from Newcastle to Throckmorton. By two miles east of the county line it can be traced along the slopes of low hills north of this highway. It then turns northward along a low bluff to disappear in the Brazos alluvium near the mouth of Boggy Creek. During this segment of its course the Camp Colorado is gradually losing its calcareous nature and is in process of changing into a sandstone.

The Camp Colorado reappears on the east bank of the Brazos a mile to the north, in a low bluff west of the mouth of Rabbit Creek. It is obscure in crossing this creek, but east of this it ascends up a small tributary of the creek to the divide between Rabbit and Paint creeks, with a large outlier to the south. It then runs about three miles to the northeast along the west slopes of the Paint Creek valley, crosses this creek and swings east and south to a prominent south-facing bluff on the Jeffries ranch. Here it sharply reverses direction, and runs north and somewhat east, descending to cross Salt Creek somewhat over a mile south of Olney. East of Salt Creek it swings for a mile up the valley of Willow Pond Creek, then turns back southwest to run eastward along gentle slopes for two miles to Pleasant Valley church. It then turns northward and somewhat eastward (poorly exposed) for two miles to gain the east-west ridge separating the Brazos drainage from that of the West Fork of the Trinity River. It crosses to the north through a low spot in this ridge, but outliers extend eastward along this ridge for about four and one-half miles. The main outcrop turns west, not far from the Young-Archer County line, to swing around the headwaters of the South Fork of the West Fork of the Trinity River. It continues northeastward for about eight miles down the west side of this fork, with conspicuous outliers on the east side of this creek. Crossing the West Fork proper, it continues eastward on the side of this small river, keeping at a level of about 1,050 feet not far from the creek for about 10 miles. Beyond this point the West Branch is gradually descending and swinging to the southeast and the Camp Colorado, keeping at roughly 1,050 feet, gradually diverges from the river, running some distance up Waters Branch and Darnell Branch as it approaches the Archer-Clay County line. It runs eastward north of Antelope and here meets the westward end of a line Pss, traced by McGowen for the Sherman Sheet of the Texas geological map mentioned earlier. From this point eastward my tracing of the Camp Colorado outcrop and McGowen's Pss coincide almost perfectly (except that I am doubtful of certain southern outliers of his where, I think, the south-to-north dip of the beds is not fully taken into account). The outcrop continues eastward close to the Jack County-Clay County boundary, at an elevation close to 1,050 feet. It dips northward up the valley of Flat Creek, just east of Antelope, farther to the north up the valley of Willow Creek, west of Shannon and again up a small valley near that settlement. The outcrop continues east, at the top of low south-facing hills, turning north up the valley of Turkey Creek west of Prospect and, to a lesser degree, up a small branch east of that settlement. It then runs south two and one-half miles to a hill two miles west of Postoak and then runs northeast along the west slopes of Jones Creek for a half a dozen miles. Thence it continues eastward in an irregular course, again capping south-facing hills, for another half dozen miles, entering the drainage of Big Sandy Creek north of Newport. Near the Clay-Montague County line it turns west up the valley of Prairie Branch; it then follows eastward down the north side of Prairie Branch to about the county line, then retreats northwest up a branch of this creek toward Vashti before returning eastward, and, after some miles, turning for some distance up East Prairie Branch for about one and one-half miles. East of this creek it runs eastward along bluffs well north of Lake Amon G. Carter (with a deep "incision" for Trail Creek). West of Briar Creek it swings northward for about four and one-half miles to a point west of Bowie, and then, after returning some distance down the east bank of this creek, turns eastward to end beneath the Cretaceous cover.

Sedwick Limestone

Sedwick limestone, being the upper element of the Moran Formation is, again, well developed in the counties to the southwest of the region with which we are here concerned. It is shown, in somewhat incomplete fashion, on the 1937 Throckmorton County map (Hornberger, 1937), running north and somewhat east toward Elm Creek. I began tracing this limestone at a point about two and one-half miles west of the Young-Throckmorton County line, and about three miles south of Elm Creek. The Sedwick here is following north a ridge between Meyers Branch and an unnamed small creek to the west. With a slight interruption the Sedwick follows this ridge to within about half a mile of Elm Creek and then turns back southwest to a crossing of this unnamed creek. I could not trace the Sedwick down the even slopes west of this creek until, within about a mile of Elm Creek, the limestone is seen on a low ridge. The Sedwick then turns back southwest, east of Bush Knob Creek, to cross that creek at about three and one-half miles south of its mouth. Subsurface logs indicate that it again turns northward, but I found no surface indication of it until it is exposed in the bed of Elm Creek at a ranch road crossing some miles to the northwest.

North of Elm Creek, in a fashion comparable to the Camp Colorado a few miles to the east, indications of the limestone gradually become apparent, and it gradually ascends the north slopes of the Elm Creek Valley in a zig-zag fashion, until, about a mile west of the county line, it crosses north out of the Elm Creek drainage into that of small western tributaries of the Brazos, along which it runs northward to Boggy Creek, east of Elbert. In this stretch the Sedwick maintains its character as a somewhat sandy limestone, and is accompanied by a shale layer containing *Myalina.* At Boggy Creek it turns westward, and is traceable to a point south of Elbert. It is not exposed north of the creek, although the *Myalina* bed is definitely present. Two miles east of Elbert the Sedwick again becomes visible and can be followed to the west for three miles to a point south of Leopard Creek. For the next four miles north and northeast to a bluff on the west bank of the Brazos, little is seen of the Sedwick (now a calcareous sandstone), for a curious reason. A local rancher, now deceased, had apparently become deranged from his services in the First World War, and seems to have spent most of the remainder of his life building beautiful stone walls (which have no obvious function) and appears to have incorporated in them nearly all sandstones visible in the area.

The Sedwick appears at the base of the bluff mentioned above, and then disappears into the Brazos bottoms. A mile to the north, somewhat over a mile below the Spring Creek settlement, the Sedwick is seen emerging along a low bluff. From this point it runs eastward and northward, crossing Spring Creek and then following the north side of Bitter Creek. This is farming country, but the general course of the Sedwick can be followed from slabs of calcareous sandstones seen here and there in the fields and field margins. South of Bitter Creek are low hills, capped by sandstones that are obviously Sedwick outliers. More important, well logs strongly indicate that the sandstones capping the hills west of Padgett, several miles to the south, are also Sedwick outliers.

The Sedwick crosses Bitter Creek about four miles east-northeast of Spring Creek settlement and then turns south to become clearly visible in slopes lying along the Olney-Spring Creek highway. Farther east the country is quite flat, exposures are rare, and were it not for the aid of well logs it would have been extremely difficult to follow this bed. The course is slightly north of east, into the northwestern end of the Salt Creek drainage, to a point at the west end of the settled Olney area, then north past the Lutheran church into Archer County. The course now runs north along the west side of a narrow valley which is running northward toward the Little Wichita River. East of this valley there develops a large outlier bounded (except to the south) by well-developed bluffs. The main outcrop follows the valley northward to about four miles north of the Young-Archer County line, then turns southwest, circling most of the headwaters of

Mesquite Creek and the two Olney reservoirs. Following down the west side of these reservoirs, the outcrop continues north close to the paved north-south road (farm road 2178) for two and one-half miles, then turns east along the low divide between Mesquite Creek and the South Fork of the Little Wichita River to the region of their junction. Here the outcrop is nearly lost in the alluvium, but having crossed Cottonwood Creek, it runs southeastward east of that creek (with outliers to the south). South of Bobcat Bluff the outcrop swings east and north to the region of the former settlement of Anarene. We find here the watershed between the West Fork of the Trinity to the south and creeks tending north to the Little Wichita. The divide is marked by a west-east line of hills, and a long series of Sedwick outliers runs eastward along them to (and a bit beyond) the Archer-Clay County line. From Anarene the main outcrop (poorly indicated for some distance) runs northeastward down the west side of Onion Creek. The northern dip of the Sedwick and the gentle gradient of the creeks running north to the Little Wichita are almost equivalent, and the course of the Sedwick to the east, all the way to Montague County, is a complicated one, the outcrop dipping to the north in each creek valley, and returning south between creeks. The outcrop follows Onion Creek north to a point four miles southeast of Archer City, then retreats southeast for three and one-half miles, only to turn north again, to follow Little Onion Creek to within a mile of the Archer City-Windthorst highway. After a short retreat to the south, it again advances northward down the valley of West Little Postoak Creek to a point north of the highway. It then turns south, circling the Windthorst hill, and then (with faint outcrops for the most part) follows a tortuous course — for a short distance north down a tributary of East Little Postoak Creek, and, further to the east, a mile or more down the valley of that creek. East of Windthorst I find the west termination of McGowen's trace of his sandstone Pl, and his line is thus that of the Sedwick east of here.

The Sedwick sandstone now travels southeastward for half a dozen miles, with a major outlier to the south, paralleling the course of East Little Postoak Creek upward to its headwaters. Turning east, it dips slightly into the headwaters of Deer Creek, and then runs eastward to the East Fork of the Little Wichita. Here it performs a complicated course. The Sedwick Sandstone runs north some miles down the west bank of the fork, then turns back west up Joy Creek past the settlement of that name; then back down the valley of the Fork five more miles, and up a western tributary to Midway School. Finally, after continuing obscurely some distance farther down the west side of the Fork, it turns southeast and ascends the east side of the East Fork Valley for some eight miles, leaving to the west a substantial outlier in the region of Friendship cemetery. From a point about two and one-half miles northwest of Vashti, it turns northward a short distance down Smith Creek, and then east across the Clay-Montague County line. The main line of outcrop now extends eastward across the headwaters of Belknap Creek, a southern tributary of the Red River, dipping down to the north along this creek and several of its tributaries before reaching the cover of the Cretaceous about five miles north of Bowie.

Coleman Junction Limestone

Capping the Putnam Formation and underlying the Admiral, Coleman Junction Limestone is shown with a considerable degree of accuracy on the geological map of Throckmorton County (Hornberger, 1937), running north-northeast from a point a short distance east of Throckmorton City to cross the Brazos west of Spring Creek settlement a few miles south of the Baylor County boundary. North of the river the Coleman Junction runs eastward, gradually rising in elevation, barely enters Young County at its northwest corner, and then continues northeast into Archer County rising gently as it goes, crossing Spring Creek and the headwaters of Bitter Creek to attain the level of the plateau east of Megargel, and, turning north, is present on eastward-facing bluffs about five miles east of Megargel (in an oil field that was highly important in the shallow oil days). The Coleman Junction has long been known to extend this far north and, as noted above, Timms in 1928 attempted to sleuth out the general continuation of this unit north, east and north to the Red River (cf. Sellards, 1933: fig. 11). Although this was hastily done, detailed tracing shows that the line he plotted was essentially correct. A sandy lime, turning gradually into sandstone, continues northeastward from this point, high up on the west slopes of the valley of the South Fork of the Little Wichita River, but gradually descending toward the left bank of the South Fork, to reach after 14 miles the west side of the fork about two and one-half miles west of Archer City, at the junction of state highway 25 and farm road 210. The outcrop turns west and then disappears into the alluvium of the Middle Fork. From this point east and northeast the line of the Coleman Junction equivalent, as proved by well logs, follows the valley of the Little Wichita east and northeast for more than 20 miles, to the one-time settlement of Halsell, in Clay County. It is possible that in part some of the lowest sandstones north of the river are at the Coleman Junction level; on the other hand, well logs prove the existence of a number of outliers of this sandstone to the south of the main "line of march," extending to the neighborhood of Archer City and to high buttes southwest of that town; further outliers are present south of the river west of Scotland.

At Halsell, exposures now concealed under the waters of Lake Arrowhead show the Coleman Junction equivalent to reappear on the east bank of the Little Wichita and run southwest, rising gently, for several miles. Emerging above the lake level, it swings east, along slopes following the north side of the Deer Creek valley which develop into good bluffs north of Deer Creek settlement. There I find the western end of McGowen's tracing of his sandstone P4, which is thus the Coleman Junction equivalent. Three miles west of Midway School the outcrop reaches a high point at the Myers triangulation marker and enters the drainage of the East Fork of the Little Wichita. The Coleman Junction now follows down the west side of this valley in an irregular northeasterly direction for about nine miles to a point opposite Kola siding on the Fort Worth and Denver railroad, and about six miles northeast of Blue Grove. From this point the main line of Coleman Junction obviously turns eastward past Kola switch and on to the bluffs three miles north of Bellevue and two to three miles west of the Clay-Montague County line. However, the northward dip of the Coleman Junction and the gradient of the East Fork are almost identical. In consequence the Coleman Junction equivalent extends northward in a complicated fashion down the valley of the East Fork and an eastern branch of this fork extends as far north as Dickworsham switch. This was obviously mapped competently by McGowen and I have not retraced this area.

At the bluffs north of Bellevue the Coleman Junction leaves the East Fork drainage for that of Belknap Creek and turns northward, gradually descending the western slopes of that valley into western Montague County (with a number of outliers to the east) and finally, about three miles east of Ringgold, disappears into the Belknap Creek alluvium and perhaps reaches the Red River, only about two miles to the north.

I have done little work east of Belknap Creek. North of a west-east line running past Belcherville and Nocona, bounded on the east by the Cretaceous and north by the Red River, is a triangular area which McGowen, I am told, found difficult to interpret and which I, studying it in more superficial fashion, found equally puzzling. A sandstone running eastward along the line mentioned is essentially equivalent to the Coleman Junction, and hence all of the area under consideration is presumably as high as the Admiral Formation, lying above the Coleman Junction, and McGowen found here several sandstone beds suggesting to him, I am told, that we are here dealing with a deltaic condition. On the other hand, Frank Gouin has pointed out to me that in the region of Lake Nocona there is a well-developed anticline, presumably connected with the Muenster arch, which brings relatively low strata to the surface. On the map I have merely indicated the lowest sandstones, which may be roughly Coleman Junction equivalents.

ELM CREEK LIMESTONE

The top member of the Admiral Formation, Elm Creek Limestone, appears on the 1937 map of Throckmorton County, running north-northeast from the neighborhood of Throckmorton to the Baylor County line not far west of the Brazos. This limestone has not previously been mapped further north. Entering Baylor County, this limestone is present in a river bluff across the river from Round Timber settlement, and is visible in a similar bluff east of the river near Round Timber. In between, however, the limestone follows a very circuitous course. It turns westward, gradually descending in elevation along the branches of Wagon Creek, and finally reaches the broad alluvial valley of the Brazos River at the foot of a bluff about two miles northwest of Round Timber. Across the river, at the mouth of a small creek two miles north of Round Timber, the limestone is seen on the north bank of the Brazos. The country from this point north and east toward Westover is flat agricultural land, but occasional exposures, mainly in highway ditches, show the Elm Creek to follow a circular course, about two miles north from the river, then about three miles east and then back southwest toward Round Timber — the limestone gaining some elevation and becoming more readily traceable in this last part of its circuit.

For several miles east of Round Timber the ground is covered by river sands and the Elm Creek Limestone is not visible. Beyond this sandy area, however, the limestone can be followed (although with some difficulty) northward a bit west of the Baylor-Archer County line to reach the west side of Briar Creek, about four miles northeast of Westover and just west of the county line. From here the limestone runs (rather obscurely) northeast, west of Briar Creek and then, a mile or so north of the Seymour-Archer City highway, turns west and southwest into the valley of Godwin Creek. Here the situation is a confusing one. The Elm Creek is here a double limestone, and the dip of the beds is almost exactly equivalent of the slope downward to Godwin Creek, so that the two beds, prominently exposed, form a confusing pattern. The two beds gradually reach the creek level about four miles southwest of their first appearance in the eastern slopes, and then run north, poorly exposed, to cross the Little Wichita River above its junction with Godwin Creek. North of the river the limestone is better exposed, and gradually ascends the slopes, and crosses Slippery Creek about five miles south of Dundee.

A mile or so east of this creek the limestone disappears and (contrary to the usual condition in the Wichita beds) has no immediate sandstone continuation. However, well logs clearly show that the bed continues east at the foot of the bluffs south of Black Flat. East of that settlement the stratum, as shown by the subsurface, is continued along the north side of the valley of Plum Creek (locally termed Rattlesnake Canyon). However, beyond this point, five miles south of Mankins, the bed disappears into the flat prairies of the Holliday Creek valley and for the next six miles can only be traced by well logs, until a sandstone at an appropriate elevation appears in the Hull-Silk oilfield three miles south of Holliday. This runs eastward for five miles, forms a conspicuous bluff, and then turns north to disappear into the Holliday Creek alluvium.

Beyond this point the main outcrop is to be found only north of Holliday Creek and, farther on, north of the Big Wichita River. However, to the northeast there is a very extensive series of outliers, covering much of northern Clay County. Along the divide between the Big Wichita and Little Wichita rivers is a scattered series of outliers, with elevations somewhat over 1,000 feet, from the northeast corner of Archer County and the southeast corner of Wichita County into the western margin of Clay County, just east of the Wichita Falls-Henrietta highway and railroad, where the sandstone is present on a low hill at about 1,030 feet.

This marks the beginning of a large series of outliers covering much of northern Clay County. The beds here are much affected by the Electra arch structure, but with one conspicuous exception (mentioned later) this structure had become inactive by the time of deposition of the Elm Creek equivalent, and the beds are almost horizontal, lacking the northern dip seen farther south; for the most part the sandstones, which I believe equivalent to the Elm Creek, average about 950 feet above sea level. Except along the Big Wichita River there are few bluffs, and exposures are far from continuous along the gently rounded hills of the region. The major outlier is one covering the higher ground extending northeastward past Dean, Petrolia, and Byers. From the southwest corner, at the county line, its borders can be followed northward and then eastward around the valley of Duck Creek, eastward and then northwestward to the region of Dean, following the upper slopes of the valley of Turkey Creek. After running eastward for nearly ten miles, the outcrop turns northwest, to circle about the Petrolia oilfield just southeast of that town. The outcrop runs eastward again for four miles before turning northward again, to run along the upper slopes of small creeks running eastward into the Red River. There are further small outliers along the high ground east of Petrolia, the last of this series only a short distance west of the Stanfield community. The east side of the main outlier can be traced as far north as Byers. The bed, however, appears to continue about two miles north of this town, and then swings sharply southwestward, east of the Big Wichita River. Exposures generally close to the 950-foot level can be followed along this course for about 14 miles, to a point two and one-half miles NNW of Dean. Here the supposed Elm Creek Sandstone equivalent, as well as beds above and below, are turned up almost vertically, turn sharply to the northwest and disappear into the Big Wichita alluvium. Subsurface maps show the presence here of a marked syncline, presumably related to the Electra arch structure but representing an "adjustment" that took place at a much later date than formation of the arch structure. Two miles southwest of this area, the presumed Elm Creek Sandstone appears again east of the Big Wichita and, running south close to the county line, reaches the hill mentioned above where the circuit of this major outlier was begun.

The main outcrop of the Elm Creek member, as determined by well logs, runs northeastward to Wichita Falls north of Holliday Creek, but is visible only in a few places north of Lake Wichita and south of Allendale. Returning westward south of the Big Wichita, it is well exposed for most of the way west for ten miles, when it disappears into the river alluvium. East of Iowa Park it appears north of the river, but there are only occasional exposures to plot its course eastward, south of Sheppard Air Force Base and the municipal airport, then on eastward north of the Big Wichita, past Friberg School and onward past Thornberry in Clay County to a point south of Charlie. East of this point the sequence is interrupted by the course of a former channel of the Red River but farther to the east, between the Red River and the Big Wichita, Pumpkin Ridge forms a conspicuous outlier. Excellent subsurface logs are present for this northernmost part of Clay County, and it is clear that the Elm Creek Sandstone turns northward, west of the old river channel and then west along the Red River bluffs (where possible exposures are largely covered by soil). Coming west into Wichita County, this member dips a bit southward into the valley of Gilbert Creek and a southern branch of this creek, and then vanishes into the Red River bottoms.

Bead Mountain Limestone

Bead Mountain Limestone, forming the boundary, has long been known to run northeast across Baylor County, and part of its course is shown on the 1937 cooperative map of that county (Garrett, 1937) and on the similar map of Wichita County. Locally it has been termed the Rendham Limestone in Baylor County and, farther north, the Beaverburk Limestone. In contrast to all lower members, it can be traced as a limestone all the way to the Red River. In southern Baylor County, it crosses the Brazos River about eight miles south of Seymour and, rising to the east, crosses Deep Creek and then forms the summit of east-facing bluffs as it runs northward on the west side of the Godwin Creek valley east of the former England settlement and the England cemetery. It crosses Daggett Creek near its head and then swings eastward for some miles (not clearly seen) and becomes exposed in bluffs south of the Little Wichita River. Turning west, it descends to cross the Little Wichita as a limestone ledge about two miles east of Fulda station on the Wichita Valley Railroad. Turning eastward it can be readily followed for some miles and then, more obscurely, it can be seen to cross the Wichita Falls-Seymour railroad and highway just east of the Baylor-Archer County line. It now turns northward, presently forming a conspicuous bluff which, in an outlier, forms the southern margin of the dam of the Diversion Reservoir on the Big Wichita River. The limestone turns west up the south side of the river, and, since the dip of the beds and the slope of southern tributaries of the river are almost identical, has an intricate pattern. The outcrop runs southward up the valley to two small creeks west of the dam and then, west of the county line, strikes the valley of Brushy Creek up which it runs almost to the height of land and the Wichita Falls-Seymour railroad and highway. It then descends again north to the river bluffs, but three miles farther west encounters Boggy Creek, up which the Bead Mountain extends for about two and one-half miles. Beyond Boggy Creek the limestone reaches the river level about a mile west of the bridge leading from Fulda to "Sweetly Cruz" camp. North of the river the limestone descends to the Diversion Lake dam, keeping (as would be expected) close to the lake level. Below the dam the Bead Mountain runs to the northeast (Fischer, 1937) along the bluffs north of the Big Wichita, for some six miles, then turns west to descend into the Beaver Creek valley, crossing that creek about two miles east of the Wilbarger County line. Its course from this point east up onto and along the ridge north of Beaver Creek and the Big Wichita, and then back south of Beaver Creek, to a point southeast of Fowlkes Station on the Fort Worth and Denver railroad, is shown on the 1937 cooperative map of Wichita County. Until this present study it was unknown beyond a point north of Beaver Creek about six miles west of Iowa Park. I have, however, been able to trace it north to the Red River. In contrast to its strength farther west, the Bead Mountain here is thin and sandy in nature. The country between this point and the Red River is flat, with few exposures, but through occasional small exposures, mainly in road cuts, I have been able to plot its general course, northward and then eastward around the headwaters of North Buffalo Creek, Lost Creek and Stevens Creek, then over a low divide to follow the north side of the Gilbert Creek valley northeast nearly to Burkburnett. The deeper beds here are much disturbed in relation to the Electra arch, but this structure appears to have become inactive by the time of deposition of the Bead Mountain, and the surface beds here are nearly horizontal. For a short distance, near Burkburnett, no exposures of the Bead Mountain Limestone are seen, but turning west, it is occasionally visible in the slopes south of Wildhorse Creek, which it crosses about two miles northeast of Clara. It then attains the south bluff of the Red River, where it is clearly visible in the cuts of two roads which descend to the river bottoms northeast of Clara. It descends to the west, and reaches the level of the Red River alluvium north and a short distance west of Clara.

LEUDERS LIMESTONE

The Leuders, now generally regarded as a formation, has long been recognized as the top of the Wichita beds, separating them from the Clear Fork. I have not studied the Leuders in detail. Several members are shown in the 1937 cooperative map of Baylor County, crossing the Brazos in the "canyon" of that river below Seymour and running north past Maybelle and the Kemp Lake dam. I do not know of any detailed mapping of the Leuders in Wilbarger County; this limestone series crosses Beaver Creek in the central part of the county and then, as stated by Wrather (1917) trends northeast toward Harrold. It appears to be represented by sandy limestones farther northeast, along the lower course of China Creek, toward the Red River.

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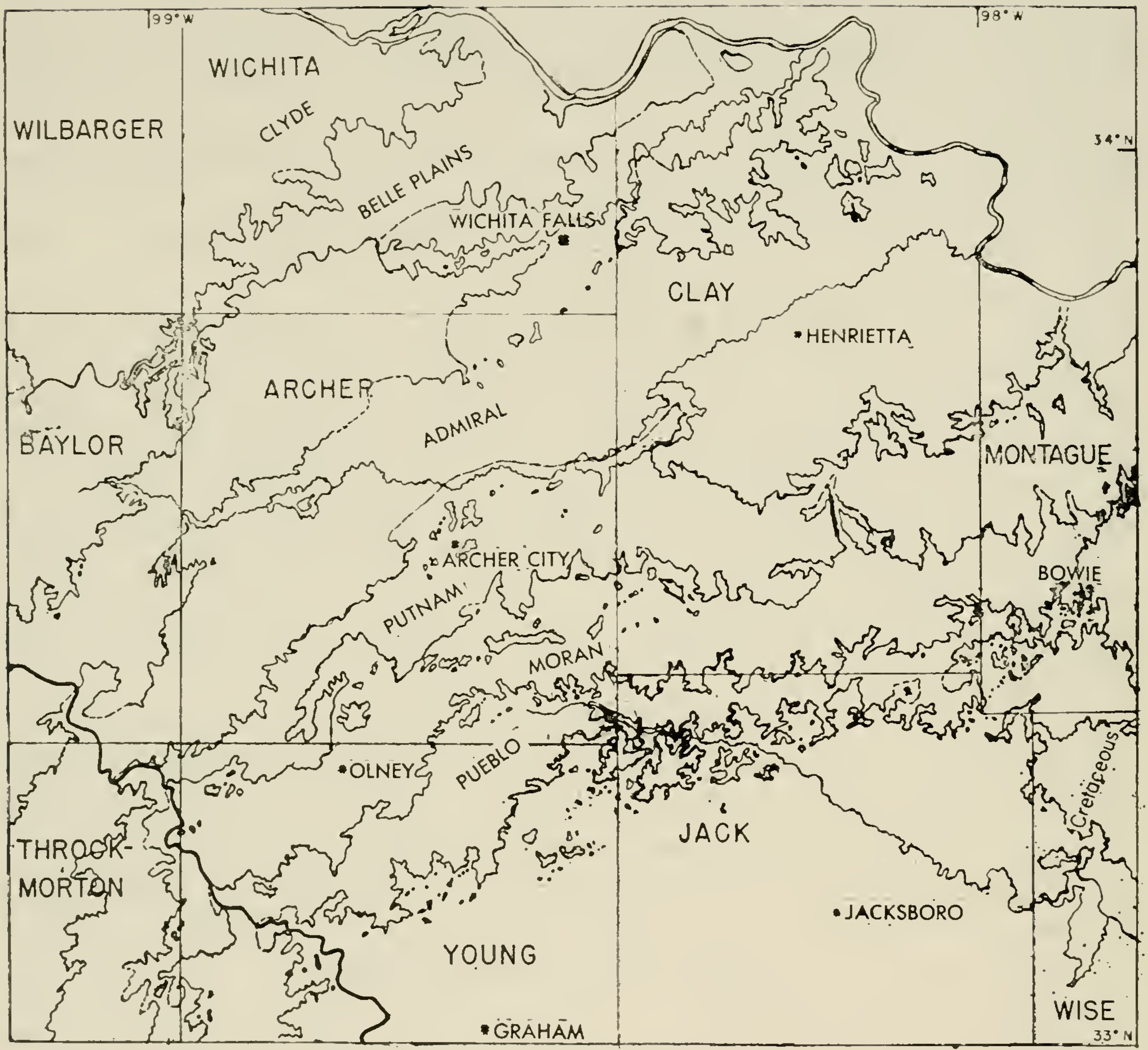
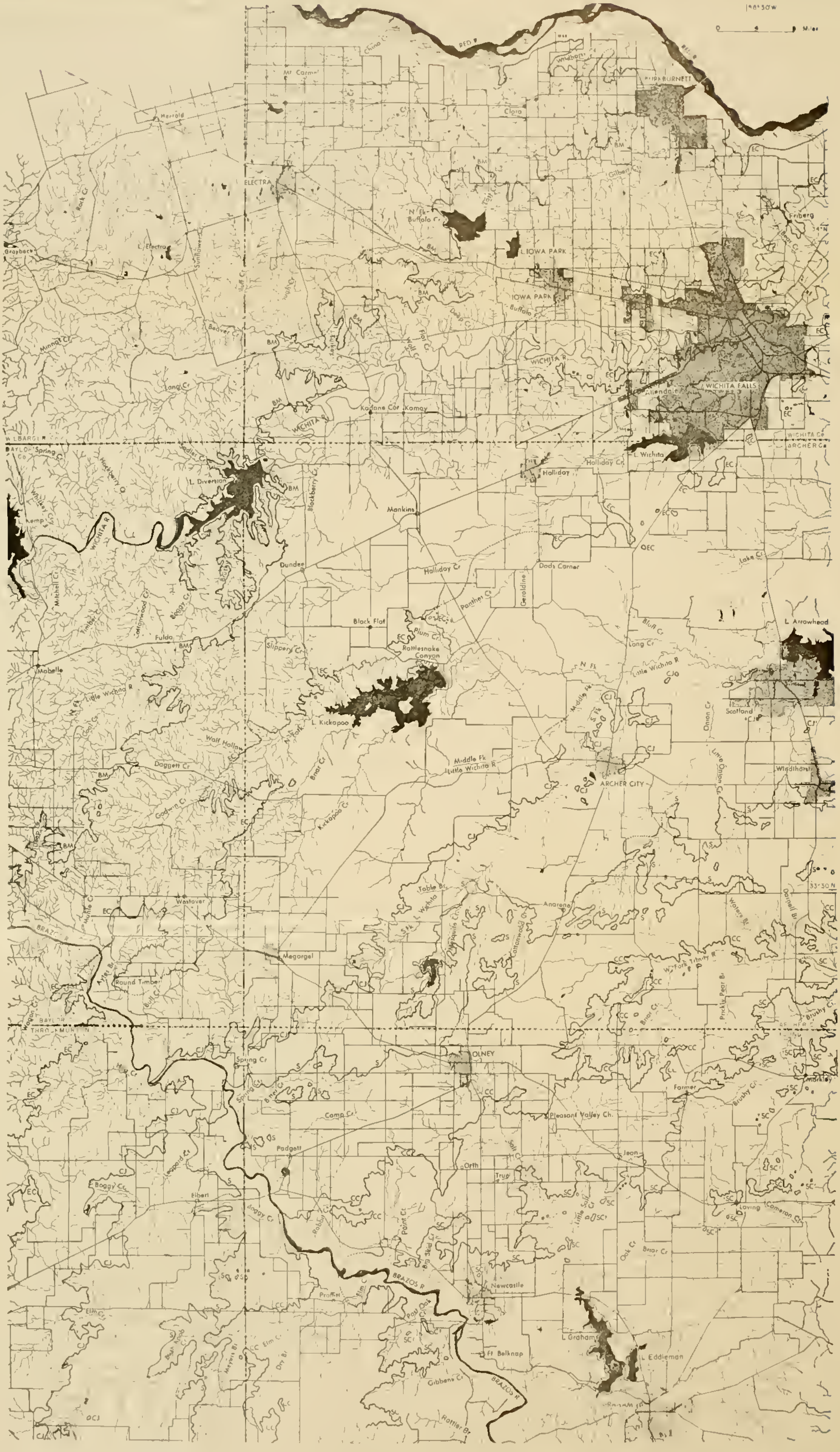
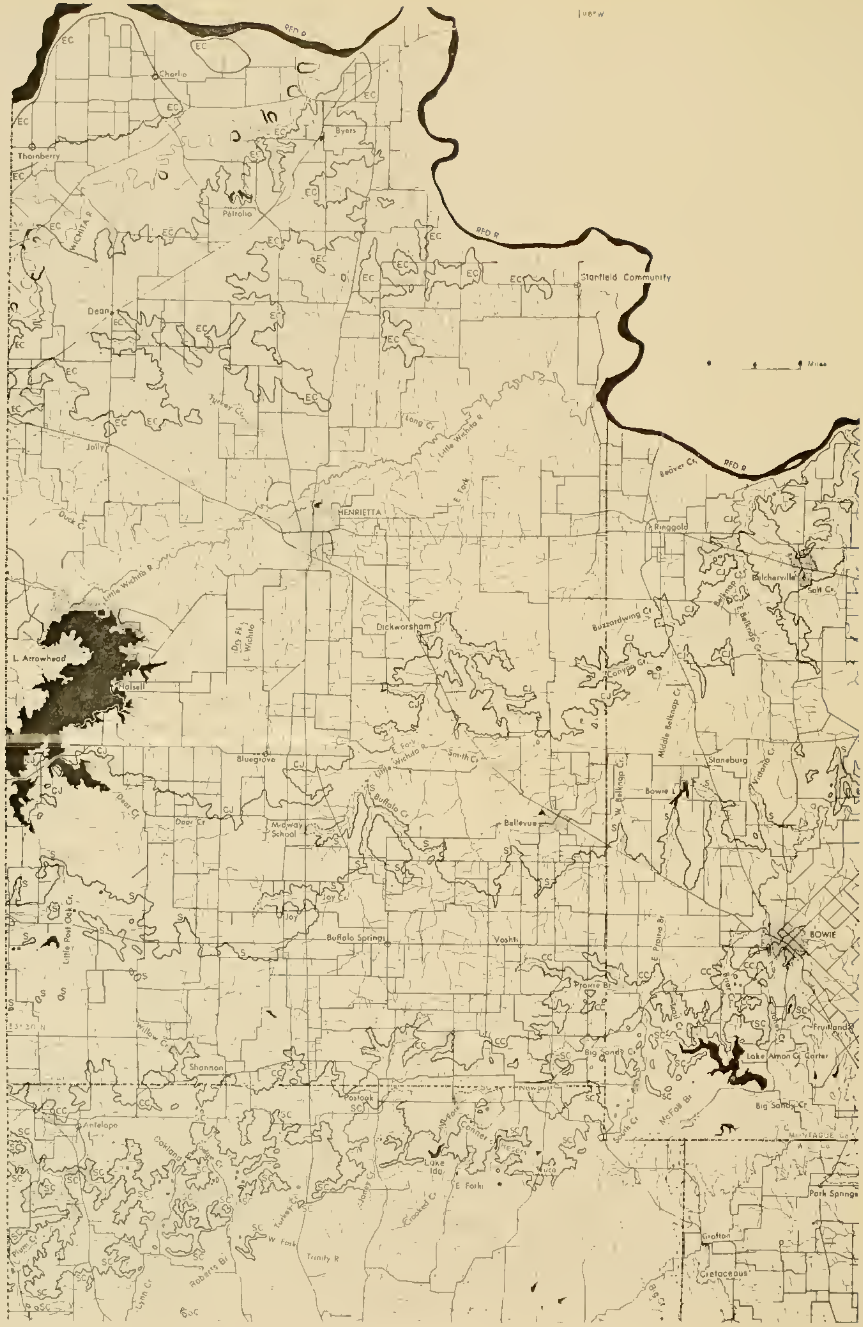

99° W
98° W
34° N
33° N
WILBARGER
WICHITA
CLYDE
BELLE PLAINS
WICHITA FALLS
CLAY
HENRIETTA
ARCHER
ADMIRAL
BAYLOR
MONTAGUE
ARCHER CITY
PUTNAM
MORAN
BOWIE
OLNEY
PUEBLO
THROCK-MORTON
JACK
Cretaceous
JACKSBORO
YOUNG
GRAHAM
WISE

Map. 1. General area of north-central Texas showing where members of the Wichita redbeds are exposed.


98°30'W
0 4 8 Miles
RED R
BURKBURNETT
Friberg
34°N
Bear Cr
Mt Carmel
Chino Cr
Clara
Herrold
ELECTRA
Graybeck
L Electra
Rock Cr
Sunflower Cr
Bluff Cr
Beaver Cr
Minnie Cr
Long Cr
N Fk Buffalo Cr
L IOWA PARK
IOWA PARK
Buffalo Cr
Gilbert Cr
Dodd Cr
Flat Cr
Wolf Cr
WICHITA R
WICHITA FALLS
Allendale
Kadane Cor
Kamay
WILBARGER Co
BAYLOR Co
WICHITA Co
ARCHER Co
Spring Cr
Blackberry Cr
Whiskey Cr
Kemp
L Diversion
Holliday
Holliday Cr
L Wichita
Mankins
Dundee
Dods Corner
Lake Cr
Mitchell Cr
Cottonwood Cr
Boggy Cr
Fulda
Black Flat
Geraldine
Panther Cr
Plum Cr
Rattlesnake Canyon
Slippery Cr
Mabelle
Little Wichita R
L Kickapoo
Bluff Cr
Long Cr
L Arrowhead
Scotland
Onion Cr
Little Onion Cr
Windthorst
Wolf Hollow
Daggett Cr
Middle Fk Little Wichita R
ARCHER CITY
Briar Cr
Kickapoo Cr
Westover
Megargel
Table Br
Anarene
Cottonwood Cr
Dornell Br
33°30'N
Waters Br
W Fork Trinity R
Prickly Pear Br
BRAZOS R
Round Timber
Bull Cr
BAYLOR
THROCKMORTON
OLNEY
Farmer
Brushy Cr
Spring Cr
Comp Cr
Pleasant Valley Ch
Padgett
Orth
Salt Cr
Jean
Loving
Cameron Cr
Fibert
Boggy Cr
Point Cr
Big Skid Cr
Newcastle
Briar Cr
Oak Cr
Elm Cr
Proffitt
Post Oak Cr
Ft Belknap
Gibbens Cr
Rattler Br
L Graham
L Eddleman
BM
EC
CJ
CC
S
SC

Map 2. Western section of the region shown in Map 1, giving in detail tracings of the various members of the Wichita Formation. Abbreviations. *BM*, Bead Mountain Limestone; *CC*, Camp Colorado Limestone; *CJ*, Coleman Junction Limestone; *EC*, Elm Creek Limestone; *S*, Sedwick Limestone; *SC*, Saddle Creek Limestone; — . . . — . . . Cretaceous boundary.


98° W
RED R
Charlie
Thornberry
Byers
Petrolia
WICHITA R
Dean
Jolly
Duck Cr
Turkey Cr
Long Cr
Little Wichita R
E Fork
Stanfield Community
Miles
Beaver Cr
RED R
HENRIETTA
Ringgold
Belcherville
Salt Cr
Belknap Cr
E Belknap Cr
Buzzardwing Cr
Conyer Cr
Middle Belknap Cr
W Belknap Cr
Dickworsham
Dry Fk L Wichita
L Arrowhead
Halsell
Bluegrove
Deer Cr
Midway School
Buffalo Cr
Smith Cr
Stoneburg
Victoria Cr
Bowie L
Bellevue
Joy Cr
Joy
Buffalo Springs
Voshti
E Prairie Br
Prairie Br
BOWIE
Fruitland
Lake Amon G Carter
Big Sandy Cr
Little Post Oak Cr
Willow Cr
Shannon
Postoak
Newport
McFall Br
Antelope
Oakland Cr
Lake Ida
E Fork
Crooked C
Turkey Cr
W Fork
Trinity R
Roberts Br
Lynn Cr
Plum Cr
MONTAGUE Co
Park Springs
Grafton
Cretaceous
Big Cr
33° 30' N
EC
CJ
CC
S
SC

Map 3. Eastern section of the region shown in Map 1, giving in detail tracings of the various members of the Wichita Formation. Abbreviations: *BM*, Bead Mountain Limestone; *CC*, Camp Colorado Limestone; *CJ*, Coleman Junction Limestone; *EC*, Elm Creek Limestone; *S*, Sedwick Limestone; *SC*, Saddle Creek Limestone; — . . . — . . . Cretaceous boundary. (Ed. note: Because Maps 2 and 3 were drawn from a large number of different maps at different scales, their north south alignment is not exact.)

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A DESCRIPTION OF THE VERTEBRAL COLUMN OF *ERYOPS* BASED ON THE NOTES AND DRAWINGS OF A. S. ROMER

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Abstract. This paper includes an illustrated description of the vertebral column and ribs of *Eryops megacephalus* Cope, based principally on notes and drawings prepared by A. S. Romer. The paper examines closely regional variation in the column. The descriptions, originally written of the *Eryops* now mounted in the Museum of Comparative Zoology (MCZ 1539), are amplified by reference to other specimens. The paper includes data on growth stages and regional variation in the vertebral column and ribs, which will be useful in interpretation of *Eryops* postcranial remains.

INTRODUCTION

This publication was to have been based on collaborative work with Alfred S. Romer, but his untimely death on November 5, 1973 prevented this. Fortunately, his notes and drawings on the postcranial anatomy of *Eryops* have been available to me and are here incorporated; his handwritten descriptive working notes are only slightly modified. The paper presents a generalized description of the vertebral column of *Eryops,* and drawings of a set of presacral and postsacral ribs. The principal concern in preparing this material has been that Professor Romer's observations should be available to paleontologists. To Professor Romer's observations, I have added others which appear to be of interest.

Gregory (1951, I: 253) called *Eryops* "the best known" of all rhachitomous labrinthodonts; Williston (1914) called it "the most famous" of the Temnospondyli. But despite the detailed descriptions of various parts — skull (Sawin, 1941), teeth (Stick-

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ler, 1899), forelimb (Miner, 1925), ilio-sacral attachment (Olson, 1936a) — no account of the vertebral column as a whole is available.

In familiarizing myself with *Eryops* material, I gratefully acknowledge the help of discussions with Ernest E. Williams, Nelda Wright, Robert L. Carroll, Thomas S. Parsons, John R. Bolt, Keith S. Thomson, Bryan Patterson and Bobb Schaeffer, and to Carroll, Patterson, Williams and Wright I extend thanks for critical reading of all or of large portions of my manuscript. I appreciate the opportunity to study specimens in the following institutions: the Redpath Museum of McGill University with Dr. Carroll, the Cleveland Museum of Natural History (CMNH) through David H. Dunkle, the Field Museum of Natural History (FMNH) through Dr. Bolt, the Peabody Museum of Yale University through Dr. Thomson, the American Museum of Natural History (AMNH)) through Eugene S. Gaffney, and the Pratt Museum of Amherst College through Walter P. Coombs; and I was aided by valued correspondence with several of those mentioned above and also with Robert E. DeMar, Everett C. Olson, A. L. Panchen, F. R. Parrington and Peter P. Vaughn. A loan of *Eryops avinoffi* material from the Cleveland Museum is gratefully acknowledged.

The staff of the Museum of Comparative Zoology, and especially Professors A. W. Crompton and Farish Jenkins, Jr., Director and Associate Curator of Vertebrate Paleontology, have been very generous with their hospitality and have made the Museum a most rewarding place to work during spring term of 1973–74. I am indebted for travel and research funds to Bowdoin College.

Eryops material has been described from the Carboniferous and Permian of an area extending from New Mexico to Prince Edward Island (Langston, 1953, 1963; Olson and Vaughn, 1970), the bulk of it from the lower Permian of Texas where it is the common large form (Romer, 1958). Both the geological range occupied by *Eryops* and the length of time it survived are grounds for suspecting that more than one *Eryops* species existed (Williston, 1914; Romer, 1943, 1947, 1952). But in the absence of a sound anatomical basis for separating species (Romer, 1947, 1952; E. C. Olson, personal communication), the bulk of *Eryops* material from the Permian is now generally assigned to *Eryops megacephalus* Cope, 1877. Appreciation of the extent of speciation in *Eryops* must await a distinction between specific differences and those due to growth and accidents of preservation. Recognized as a distinct species, however, is *Eryops avinoffi* (Romer) from the Pennsylvanian of West Virginia and lower Permian of Pennsylvanian (Romer, 1952; Vaughn, 1958). Photographs of its dorsal vertebrae have been published (Murphy, 1971).

It is to Cope then that we are indebted for the original description of *Eryops* from Texas Permian material collected by Jacob Boll, his friend and collector (Cope, 1877; Osborn, 1931: 486), and himself a recognized scientist (see e.g. Broili, 1899: 61) and practicing geologist. Born in Canton Aargau, Switzerland on May 29, 1828, Boll died alone of appendicitis in a tent on the Pease River near its confluence with the Red River in Texas on September 29, 1880 (A. S. Romer, personal communication), lamented by his friend Cope (1884). *Eryops* material was given a prominent place in Cope's collection (Osborn, 1931: frontispiece; 587) and figured frequently in his publications. Cope's paleontological collections, purchased for the American Museum of Natural History (*idem,* Chapter 6), included materials Boll had collected. One specimen, AMNH 4183, from which I believe Cope's most frequently reproduced figures of vertebrae were drawn (see, for example, Cope and Matthew, 1915), is still accompanied by Boll's penciled, signed field label dated 1–12–80 from the North Fork of the Little Wichita River, which, together with the Big Wichita, Boll explored scientifically for over six months from December, 1879 (Boll, 1880). While studying this material in the American Museum collections on March 28, 1974, I happened to turn over the old field label, and there was a penciled poem, also signed 'Boll', which read as follows:

> "Nun wirst du mit noch manchen andern
> Zum Sitze des Professors wandern.
> Geistreich denkend wird er dich erwecken,
> Aus deinen Trümmern dich zusammensetzen.
> Der Nachwelt wird er dann erzaehlen,
> Wie du gebaut in deinen Zähnen,
> Wie du gelebt und wie verschwunden,
> Benennen dich und was gefunden."

For help in transcription, I am indebted to B. Werscheck of the American Museum of Natural History.

Cope's publications dealing significantly with the vertebral column of *Eryops* appeared in the years 1877, 1880 (a,b), 1881, 1882, 1884, and 1890, a number of them repeating the same left lateral and ventral views of portions of the vertebral column which first appeared in 1880 (Cope, 1880b); some of Cope's discussions of rhachitomous vertebrae (1878a,b; 1897; 1898) omitted them, but they finally appeared in Cope and Matthew (1915). Later diagrams of *Eryops* vertebrae or of generalized rhachitomous vertebrae, often drawn to emphasize particular points, are seldom more convincing than those Cope drew 'from life'.

Cope (1880a,b; 1881), Broili (1899), Branson (1905), Case (1911, 1915), Williston (1918), Watson (1919), Olson (1936b), Rockwell, Evans and Pheasant (1938), Romer (1947, 1966), Gregory (1951), Panchen (1967, Parrington (1967), Thomson and Bossy (1970), and Williams (1959) collectively provide a description of the *Eryops* vertebral column and its evolution, often with special attention to typical dorsal vertebrae. The papers of Cope (1880b) and Case (1911) provide the most complete accounts. Further, a paper on another rhachitome, *Edops* (Romer and Witter, 1942), makes several points about the vertebrae of *Eryops* and provides a measure of differentiation within the rhachitomes. A photograph of *Eryops* caudal vertebrae from the MCZ mount (MCZ 1539) has been published (Romer and Witter, 1941) with a description of dermal scales (see also Williston, 1915); caudal vertebrae have also been illustrated by Cope (1890). Diagrams of *Eryops* and other rhachitomous vertebrae are generally shown in lateral view; it is not easy to comprehend the three-dimensional form without the actual specimen in hand. The deficiency of anterior and posterior views is corrected by several of Romer's figures in the present paper. Anterior views of dorsal vertebrae are provided by Broili (1899) and Rockwell *et al* (1938). Branson (1905) and Cope (Cope and Matthew, 1915) show the atlas in anterior view, while Cope (*idem*) and Olson (1936b) show side views of atlas and axis, articulated and disarticulated respectively; Cope (*idem*) shows a somewhat distorted atlas (AMNH 4183) articulated with the axis in anterior view. Photographs of mounted *Eryops* skeletons have been published (Miner, 1926; Romer, 1943), as well as drawings of the entire skeleton (Case, 1911; Gregory, 1951).

An illustrated description of the whole vertebral column and ribs had long been planned by Romer (1943, 1947, 1958). His drawings with others showing particular points are here presented with a description prepared largely from his handwritten

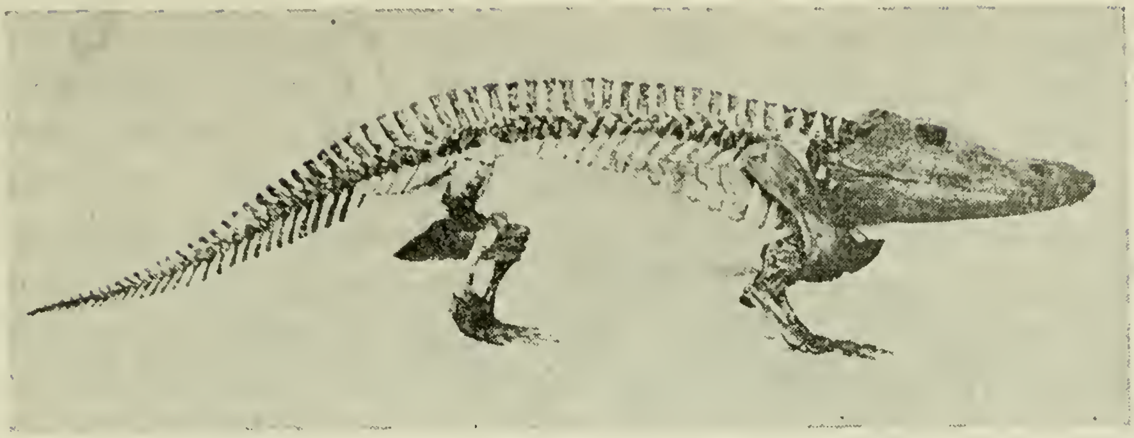

Plate I. Mounted skeleton of *Eryops,* MCZ 1539 (from Romer, 1943). × 1/21.

notes. Observations on variations in size and form in *Eryops* vertebrae are also included. A future study should focus on vertebral growth in *Eryops megacephalus,* a matter of considerable interest only touched on in the present paper. This paper examines variation in structure throughout the vertebral column, and reconstructs the probable structure in life of the vertebral column of *Eryops* from the dissociated jumble of neural arches, pleuro- and intercentra to which the vertebral column of *Eryops* and other rhachitomes is often reduced in the fossil state.

The *Eryops* mount in the Museum of Comparative Zoology (Plate I), the "most perfect (skeleton) yet discovered" (Romer, 1943), is a not quite full-grown animal (A. S. Romer, personal communication). Vertebrae of larger size and more massive construction than those in the mount are not uncommon in the collections I have studied. The MCZ mount is however comparable in size to similar mounts in the Cleveland, Field, Peabody, American and Pratt Museums collected over a considerable span of years, suggesting that full-grown (or larger species) of *Eryops* for some reason lent themselves less well to preservation or were rarer than smaller animals. The specimen in the Pratt Museum, from Geraldine, Texas, is probably the youngest of the mounts studied; it is somewhat smaller than the MCZ mount which measures over the tops of the neural spines 187.5 cm muzzle to tail tip, with a presacral vertebral column of 71.9 cm and a postsacral length of 80.6 cm. The skull measures 35 cm.

From well-preserved *Eryops* material such as that which furnished the mounts for the MCZ and Pratt Museum, Romer (personal communication) was able to "make outlines of the whole set of vertebrae, clear to the tip of the tail, and each rib";

drawings from those outlines illustrate this article. Complete tails and even complete presacral series of *Eryops* vertebrae have not been common finds, and understandably controversy has arisen over tail lengths and vertebral numbers. The MCZ mount is taken to be correct until better information is available; it displays 22 presacral vertebrae, two less than the primitive number (Romer, 1947; Vaughn, 1971), and 37 postsacral vertebrae, a total, with the single sacral, of 60. The paired proatlas atop the bisected atlas is well shown in its correct relationships in the Field and Pratt mounts (Fig. 1). Presacral-postsacral counts of five other *Eryops* mounts are: 22 — 44, 21 — 51, 22 — 30, 22 — incomplete postsacral series, and 22 — 46.

With Case (1915) we are inclined to believe that the bifurcated caudal spines in *Eryops* provided dorsal accommodation for tendons, which in primitive forms are the chief support of the axial column (Olson, 1936b); the *Eryops* arrangement suggests a tail of reasonable length which may have been held off the ground. Tail length in *Eryops* should be resolved because it is of significance in understanding locomotion. Former estimates have varied from Cope's of a medium-length tail (1880b) to a stump nearly coccygeal (1884), the latter seconded with some reservation by Case (1915), to Williston's admission of ignorance and his drawing of *Eryops* with its tail concealed by vegetation (Williston, 1914). Romer's orthometric linear unit (Panchen, 1966) has not been applied to *Eryops* in estimating a length for the tail.

The following descriptions unless otherwise stated are based on vertebrae in the MCZ and Pratt Museum mounts of *Eryops*.

PRESACRAL VERTEBRAE BEHIND THE AXIS (DORSAL VERTEBRAE)

(Figs. 1–4; 9 I; 10; 11; measurements in Table 1)

Each vertebra consists of four ossifications: neural arch, paired pleurocentra behind the neural arch and a single intercentrum ahead and below. The neural arch terminates dorsally in a neural spine that, for an amphibian, is of considerable height. In a mid-dorsal, the height of the spine above a line through the center of the zygapophyses is 56 mm, when the vertebral length is 35 mm, a ratio of 1.6. Spine height increases to 73 mm in the last presacral, and the height-length ratio approaches 2. There is a gradual decrease in spine height anteriorly — it being

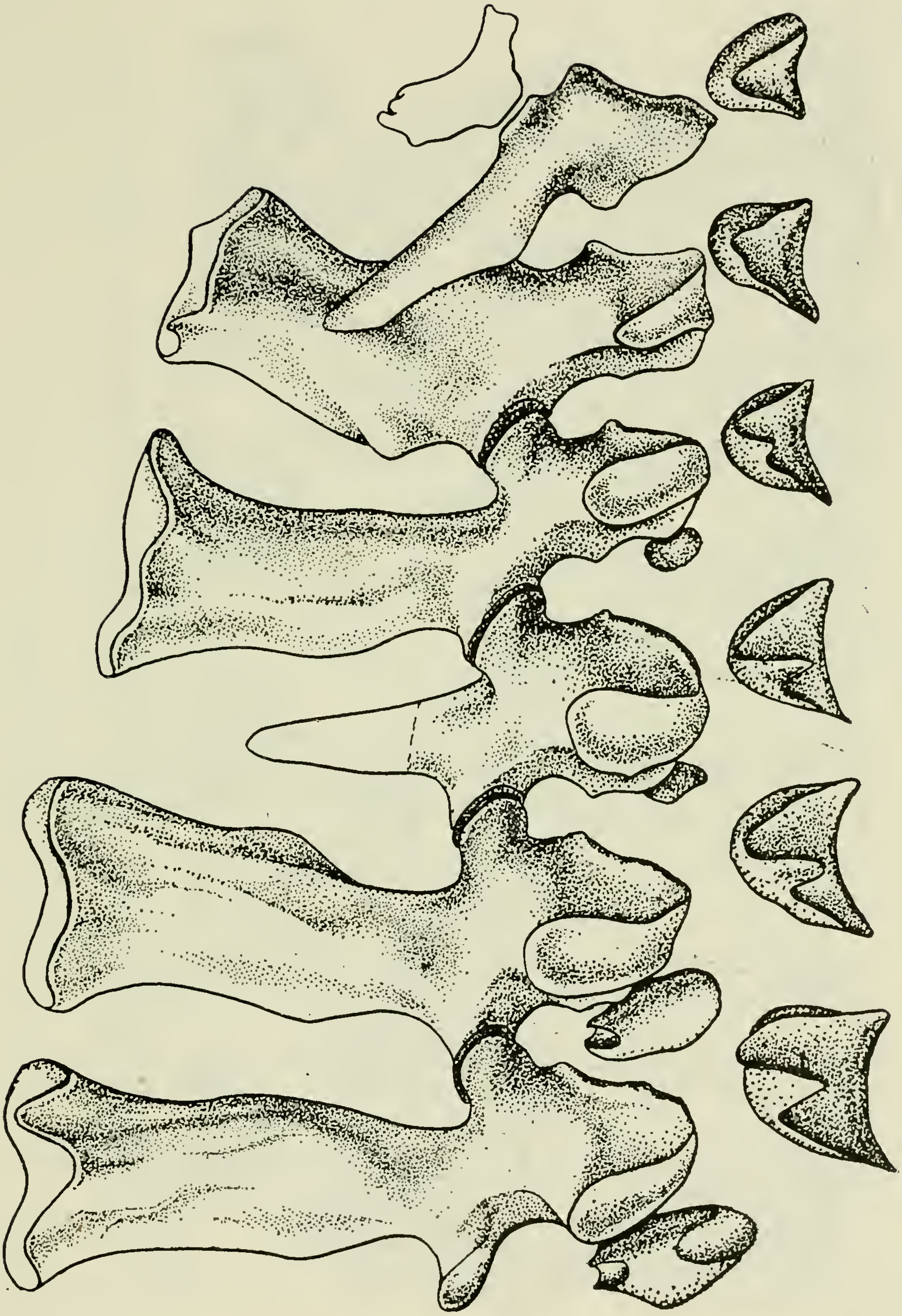

Figure 1. The presacral vertebral column of *Eryops*, anterior to the right: Proatlas, atlas, axis and vertebrae 3–6, × .9.

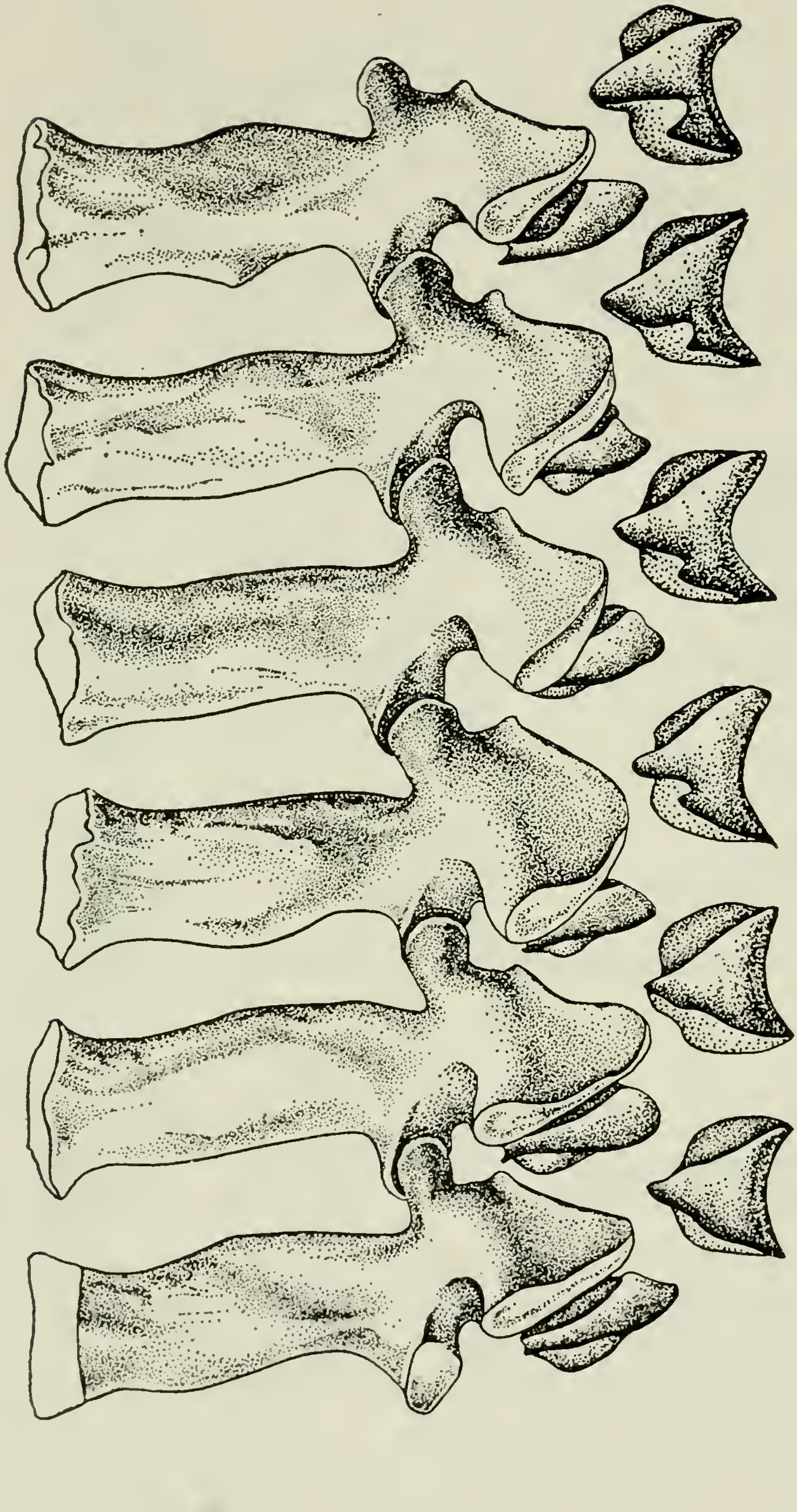

Figure 2. The presacral vertebral column of *Eryops*, vertebrae 7–12, × .7.

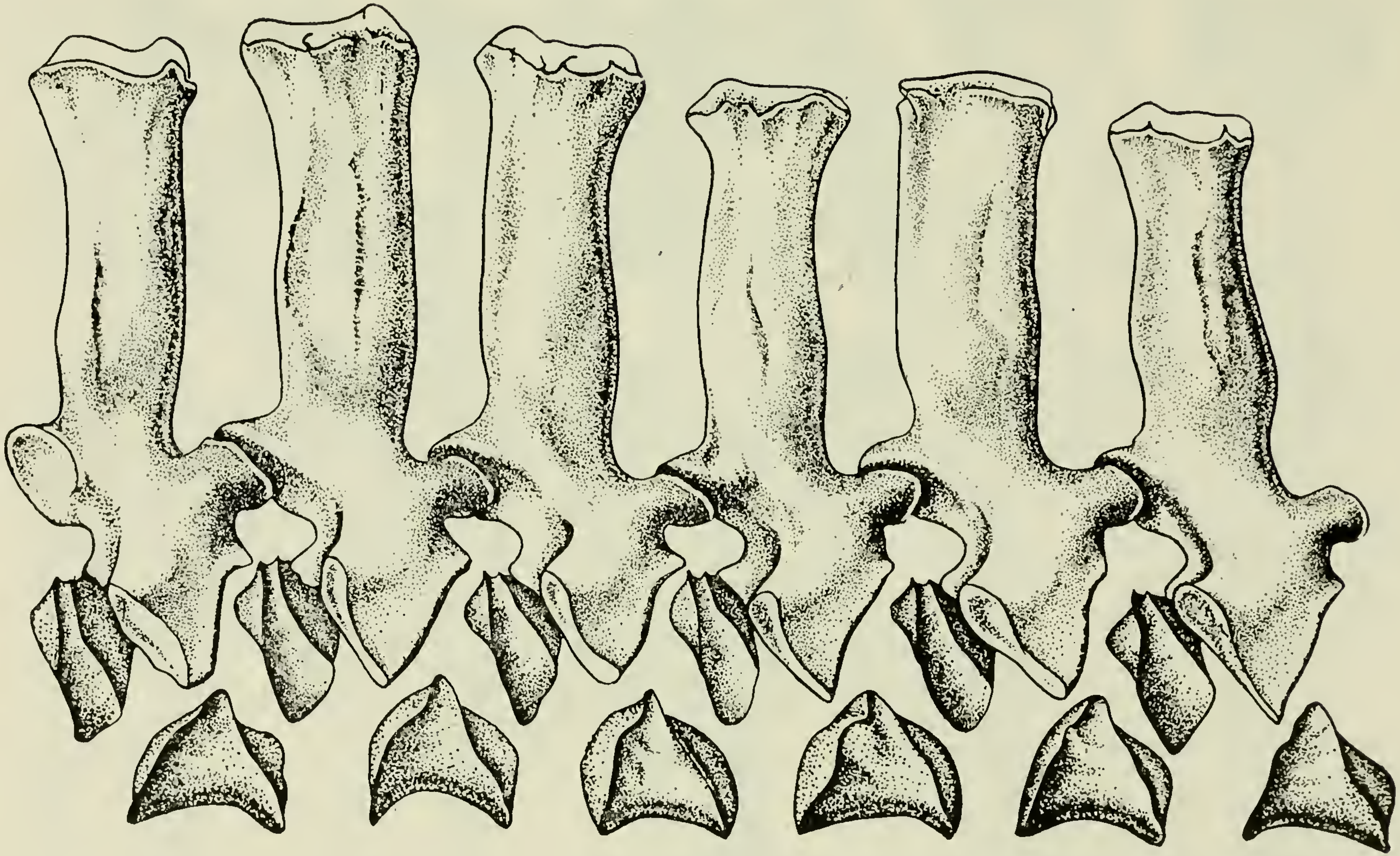

Figure 3. The presacral vertebral column of *Eryops*, vertebrae 13–18, × .7.

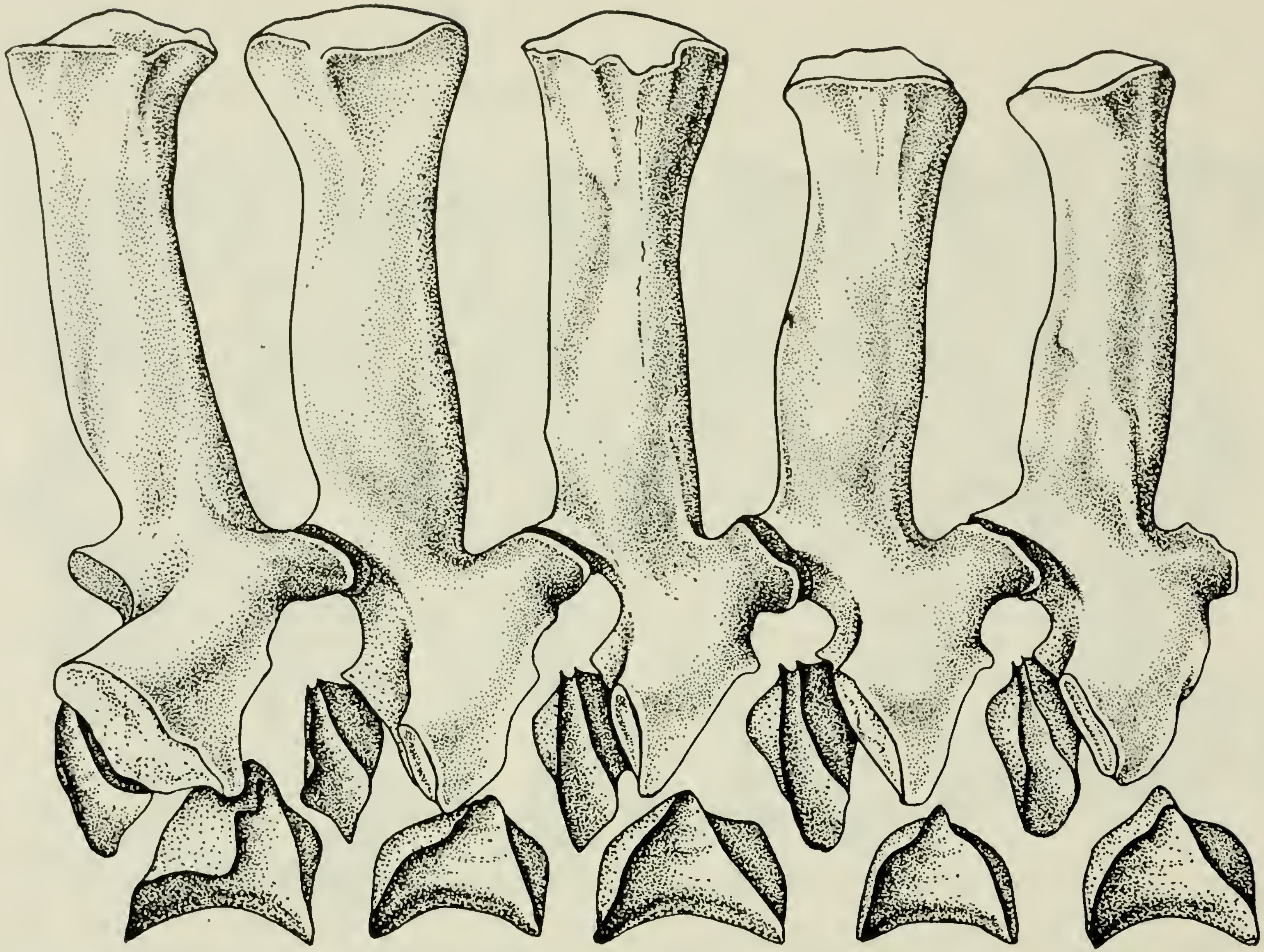

Figure 4. The presacral vertebral column of *Eryops,* vertebrae 19–23 (sacral vertebra), × .7.

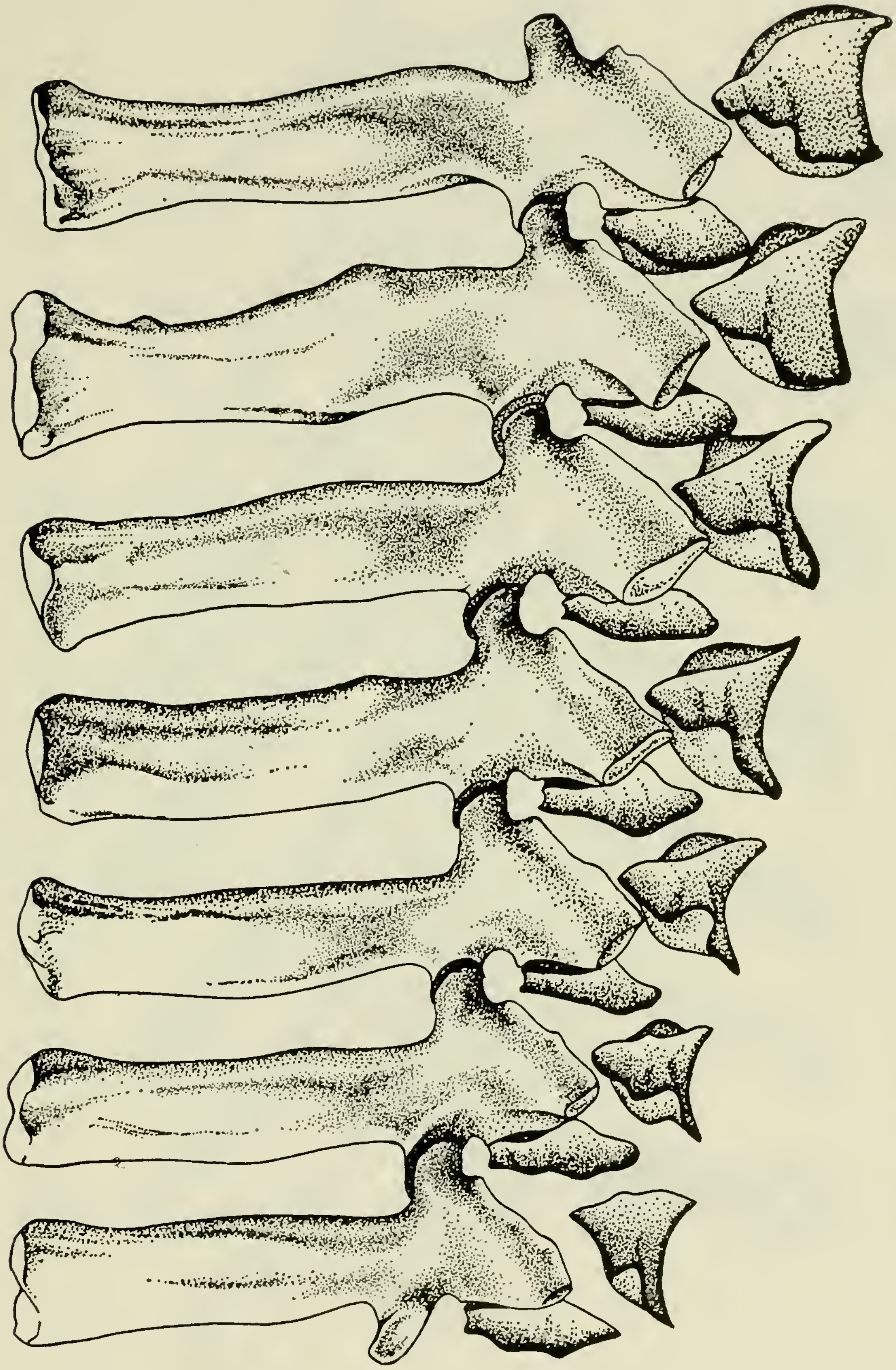

Figure 5. The postsacral vertebral column of *Eryops*, vertebrae 24–30, × .7.

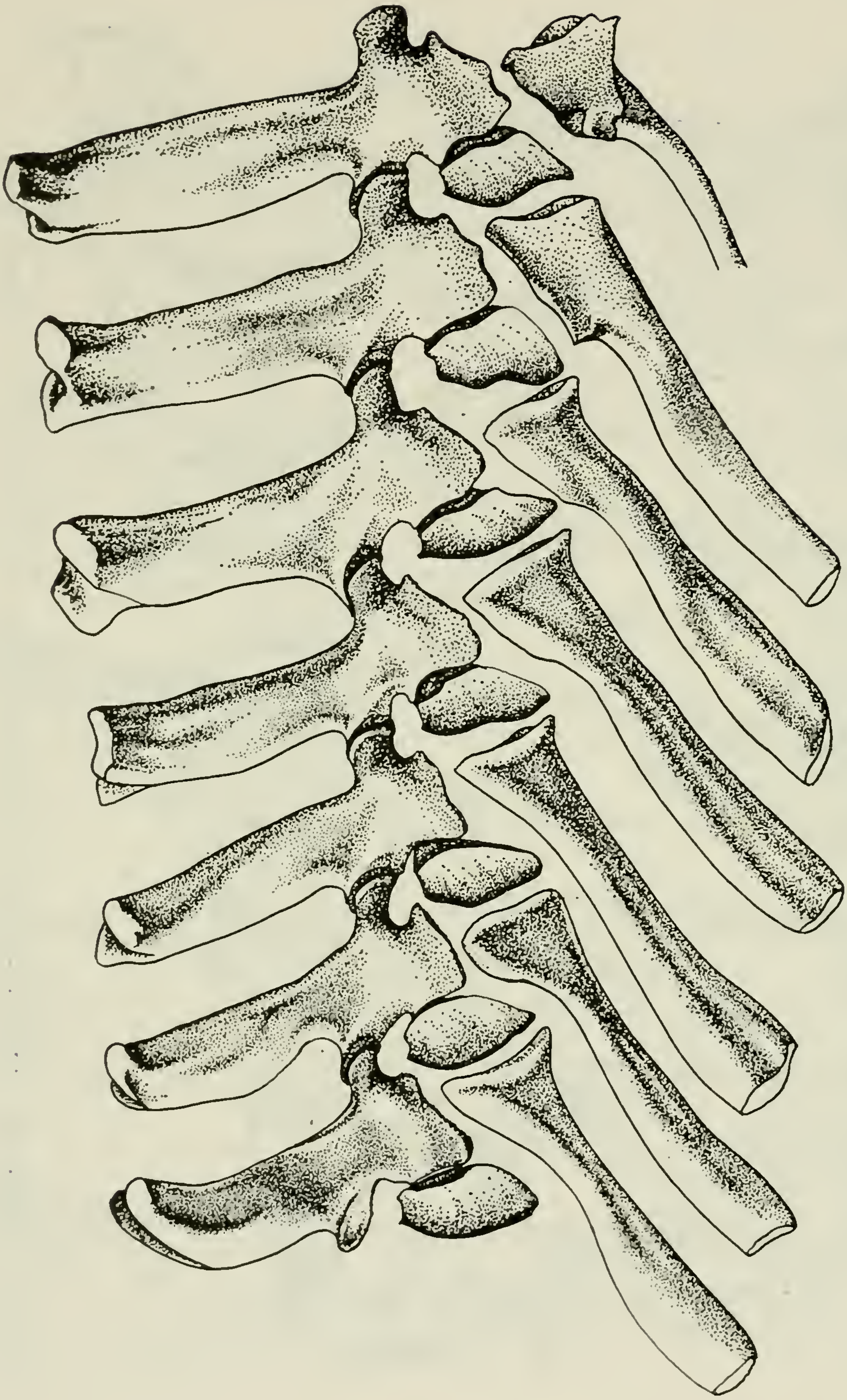

Figure 6. The postsacral vertebral column of *Eryops*, vertebrae 31–37, × .7.

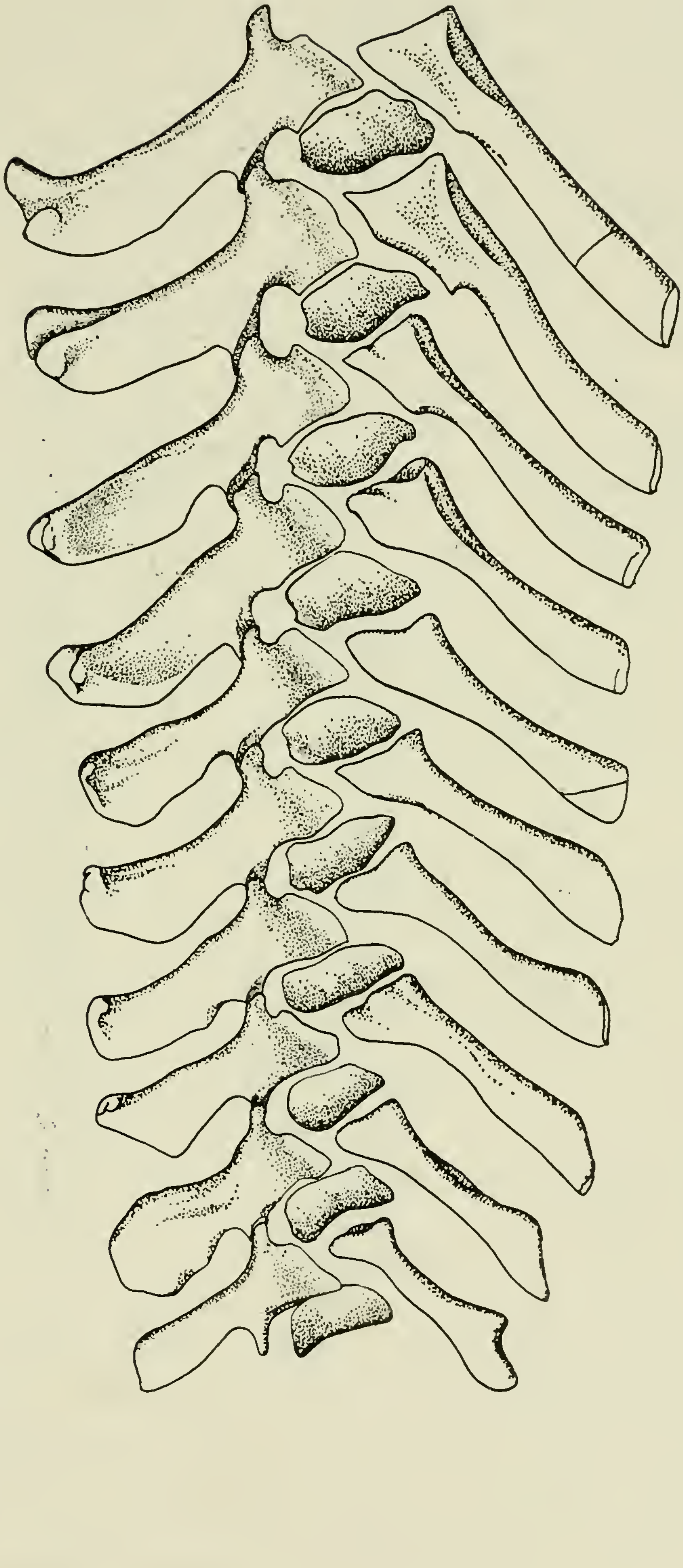

Figure 7. The postsacral vertebral column of *Eryops*, vertebrae 38–47, × .7.

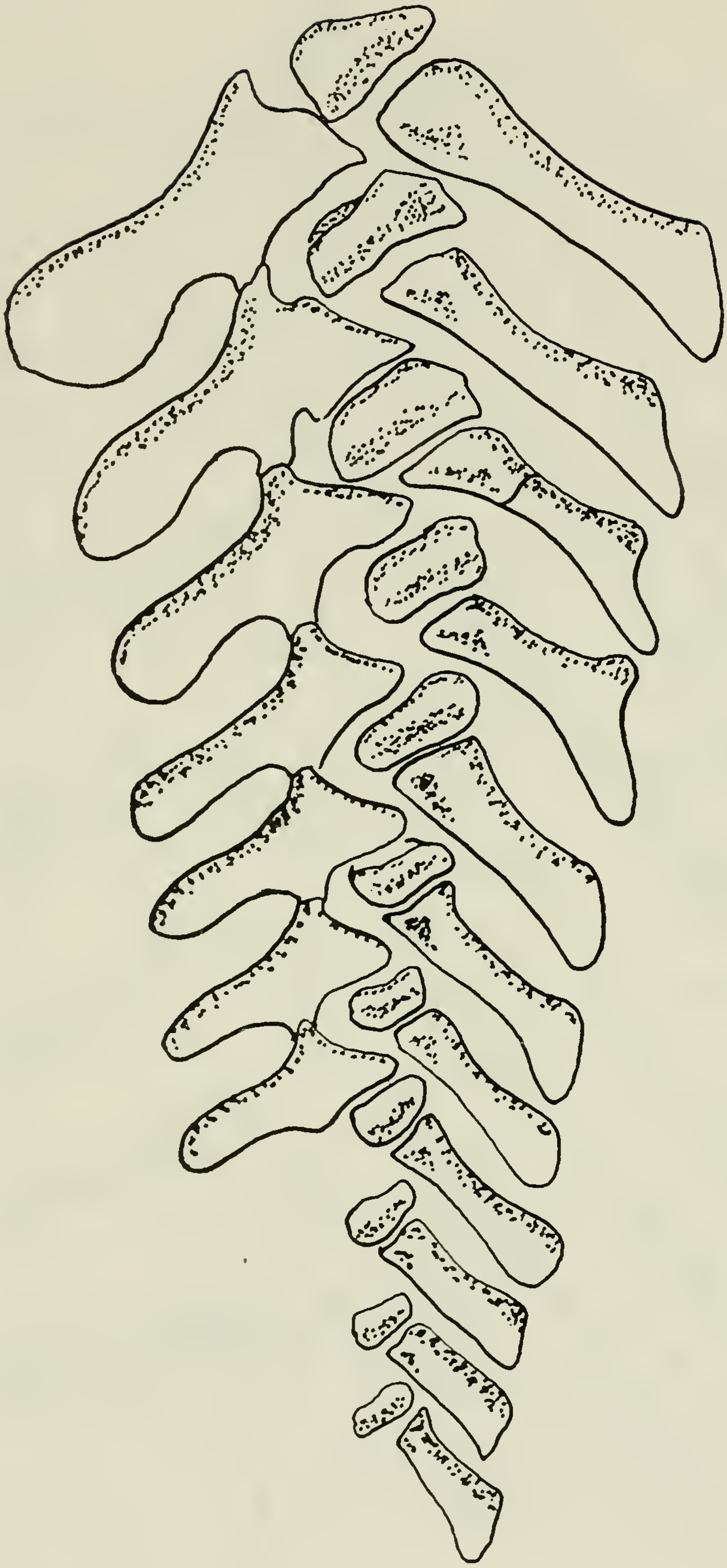

Figure 8. The postsacral vertebral column of *Eryops*, vertebrae 48–58, × 1.

57 mm in vertebra 5 — and a rather sharp decrease associated with transition to the skull, it being 44 mm at the axis.

In reasonably mature specimens, the tops of the spines become expanded, subcircular and rugose; they surely lay in the dermis. The appearance in some cases is of dermal ossifications fused to the spine tips (Fig. 14 B), but there is no evidence of separate ossifications. Expanded spine tips may be lacking in young specimens. The width of the spine shaft is about 2/3 of the anteroposterior dimension, although sometimes the neural spines are considerably more flattened than this. The spines often assume a diamond form in cross-section with lateral ridges in the upper part which expand into the sides of the dorsal rugosity.

Minor spines, spurs and flanges are not uncommon on neural spines and elsewhere (Fig. 9 I; two spines on a neural spine, AMNH 4183; spine on transverse process of vertebra 18, AMNH 4280; flange on spine of postsacral 10, MCZ 1539). Some of these may be artifacts of preservation, as is undoubtedly the flattening observed in some neural spines. A remarkable flexibility of *Eryops* skeletal material either shortly after death because of drying cartilage (see p. 22) or changes during preservation is suggested by the twisted neural arches and spines one not infrequently encounters in collections (Fig. 9 D; sacral vertebra of MCZ 2669, for example).

The upper part of the neural spine is keeled both anteriorly and posteriorly. In the lower part of the spine, the keel bifurcates into two divergent ridges which pass into the zygapophyses ventrally. Secondary ridges may be present within the groove enclosed by the ridge pairs. Both grooves tend to become reduced in depth in very large vertebrae. The anterior groove may extend more than halfway up the spine, more so in the anterior part of the vertebral column than posteriorly. In the last presacrals, the anterior groove is limited to 1/3 of the spine height and becomes relatively shallow. The point of bifurcation of the ridges at the top of the grooves is often recognizable in side view by a marked angularity in the contour of the spine, and the spine shaft is broadest between these points. The posterior groove deepens ventrally into a deep pit between the posterior zygaphophyses.

The zygaphophyses are of the normal primitive tetrapod type and are readily comparable with, for example, those of many pelycosaurs in size, contours, inclination and relative position. As usual in labyrinthodonts and pelycosaurs, but in contrast to

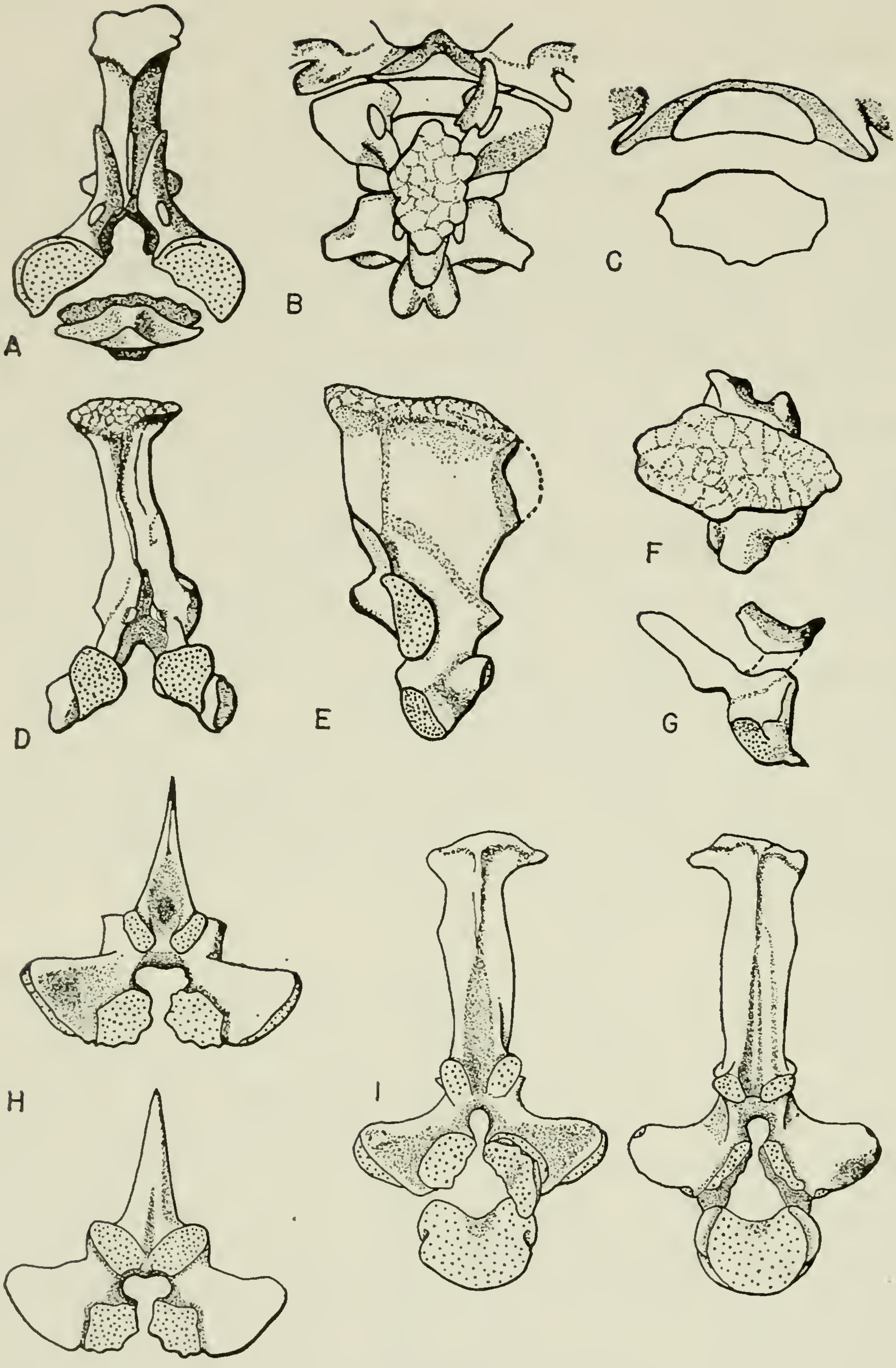

Figure 9. Based mainly on *Eryops* MCZ 1539 and 1883, all × .5. (A) Atlas and axis with their intercentra, in anterior view, proatlas removed. (B) *Eryops* occipital region, atlas, axis and right proatlas, anterior at top. (C) *Eryops* occipital region from below showing anterior intercentra. (D) *Eryops* axis MCZ 1883, anterior view. (E) *Eryops* axis MCZ 1883, right lateral view, anterior flange reconstructed. (F) *Eryops* axis MCZ 1883 in dorsal view. (G) *Eryops* atlas and proatlas, left elements from medial side. (H) *Eryops* vertebra 4, posterior (above) and anterior views. (I) *Eryops* vertebra 6, posterior (l.) and anterior views.

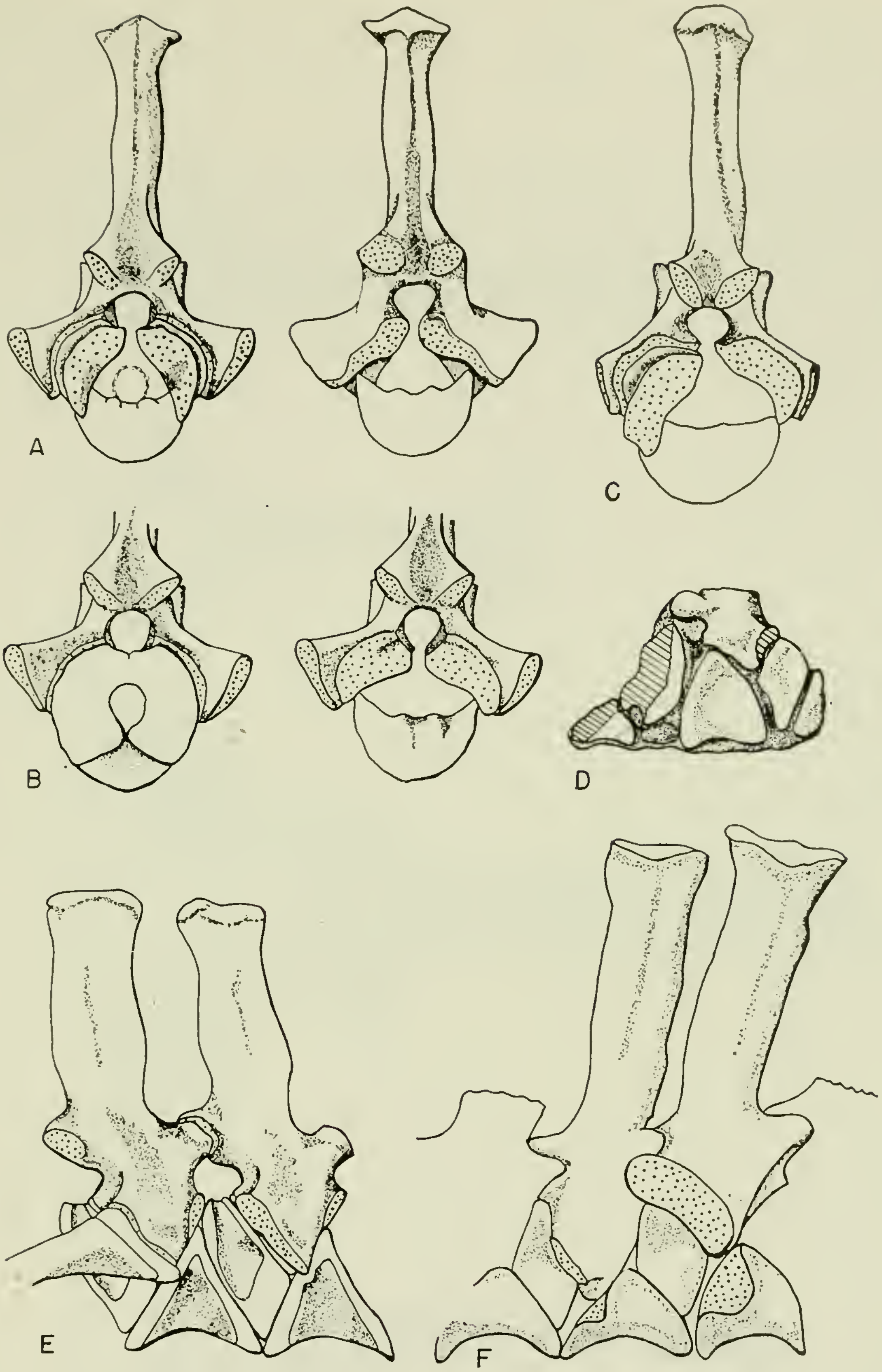

Figure 10. All × .5. (A) *Eryops* vertebra 13, posterior (l.) showing position of notochord and anterior views. (B) *Eryops* vertebra 13, posterior views, with (l.) and without reconstructed cartilages surrounding bony centra. (C) *Eryops* vertebra 21, posterior view. (D) MCZ 1828, left view, showing matrix (dark stippling) occupying position postulated for cartilage about centra of presacral vertebrae. (E) Reconstruction of two dorsal vertebrae showing cartilage reconstructed about centra and rib head. (F) *Eryops* vertebrae 23 and 24, right view, showing facets for rib articulation (large stippling).

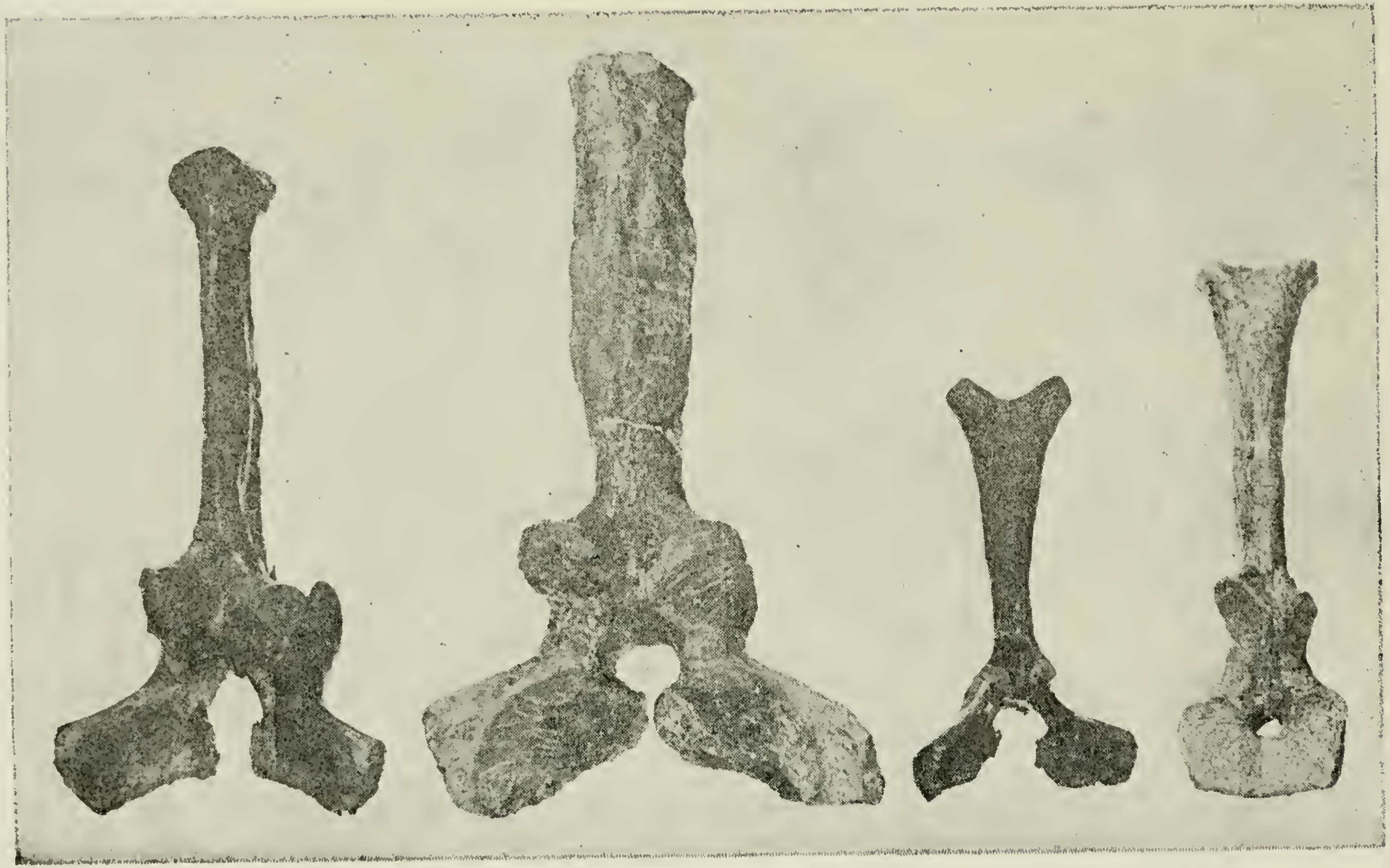

Figure 11. Smaller and larger dorsal and caudal vertebrae in posterior view showing changes in form attributed to growth, × .7.

cotylosaurs, the zygaphophyses are situated close together with but a short interval between the medial surfaces of the components of each pair. The typical dorsal zygapophyses are tilted so that the posterior zygaphophyses face about 45° out from the median plane and 45° up from the horizontal plane, and diverge 30° laterally from the median plane; the anterior ones face 45° in, 45° down and diverge 30° laterally. The angles of the zygapophyses vary somewhat throughout the length of the column, the posterior zygapophyses tending to be nearer the horizontal and smaller anteriorly than posteriorly. The face of the posterior zygapophyses is quite flat throughout, the anterior concave.

Continuing to consider a mid-dorsal vertebra, below the level of the zygapophyses the neural arch divides into two pedicels; between them these form a well-defined roof and lateral walls for the neural canal, which is subcircular in outline, as the center of the floor is unossified. The degree of closure of the pedicels below the neural canal, however, is a function of age and size or both (Fig. 11). One can demonstrate sacra (MCZ 2604, 4305) and a caudal vertebra (MCZ 3316, Fig. 11) with a completely ossified neural canal, and a whole series of dorsal vertebrae in which it is nearly closed ventrally (MCZ 3316, Fig. 11). Where the floor is unossified, cartilage probably formed a ventral apex to the neural arch between intercentrum and pleurocentrum in life.

Laterally, the surface between the anterior and posterior zygapophyses is smooth, but there is a depression, usually rather shallow, behind and below anterior zygapophysis. At about the midpoint of the length of this depression a ridge develops that swings down and back into the dorsal edge of the transverse process, presumably associated with the passage of a segmental blood vessel.

The anterior and posterior margins of adjacent vertebrae, below the zygapophyses, form the posterior and anterior margins respectively for the intervertebral gaps that afforded exit for the spinal nerves. These margins do not, however, form ventral boundaries for the gaps.

The posterior surface of the neural arch on each side, from the level of the neural canal floor down over the pedicel, includes a very large unfinished area which faces as much inward and downward as backward. It is subquadrate in form, but rounded in the dorsolateral margin. This surface corresponds to that on the anterior surface of the pleurocentrum and is articulated with the anterior face of that element, although obviously with an intervening thickness of cartilage. The roughened anterior face of the pedicel, continuous with the posterior face at the ventral edge, is much smaller and irregularly shaped. The upper portion, adjacent to the spinal canal, is subcircular with a pronounced convex mass of bone projecting backward and inward. The more ventral portion of this surface slants downward and outward, narrowing rapidly, becoming concave rather than convex, and twisting so as to face a little inward. This surface matches the posterior face of the next anterior pleurocentrum to a moderate degree and undoubtedly apposed it; there must have been a considerable thickness of cartilage between the two.

The transverse process is rather variably developed. It is typically wedge-shaped in section and at the distal articular surface broad above, narrower below. Typically, the dorsal margin arises in a ridge projecting laterally beyond the surface of the arch pedicel. It faces backward and downward so that the articular surface in a mid-dorsal vertebra faces back about 40° and about 30° downward, in anterior vertebrae more directly laterally.

In a mid-dorsal, the articular surface for the rib extends downward to form the most ventral part of the arch ossified; typical anterior vertebrae are similar. Posteriorly the articular area becomes reduced to the dorsal part of the articulation. In more anterior dorsals, there are two distinct portions: (1) a broader oval dorsal area meeting the tubercle; (2) a thinner ventral extension. Posteriorly, the ventral part disappears and the upper part becomes thin; anteriorly the upper part remains thick and the ventral part tends to thicken as well, until the articular surface becomes a unit.

The measurements of *Eryops* dorsal vertebrae presented in Table 1 are based on AMNH 4280, which includes a set of dorsal vertebrae to which definite numbers can be assigned, and MCZ 1539, the mounted specimen. From the information provided by these two specimens, it has been possible to estimate the position of isolated *Eryops* presacral vertebrae through the size ranges most abundant in collections I have studied. Measurements of isolated *Eryops* vertebrae have been published by Cope (1877, 1878a,b) and Case (1911).

Table 1. Some Measurements of *Eryops* Dorsal Vertebrae

Vertebra number	Length of rib articular facet on transverse process (AMNH 4280)	Inclination from vertical of rib articular facet (AMNH 4280)	Greatest width of articular facet (AMNH 4280)	Height of neural spine above angle with anterior zygapophysis (MCZ 1539)	Distance from atop rib articulation to top of neural spine (MCZ 1539)	Greatest length of vertebra at zygapophysis tips (MCZ 1539)
1	—	—	—	—	—	—
2	—	20°	8 mm	—	59 mm	—
3	—	15°	8 mm	50 mm	70 mm	—
4	—	20°	16 mm	c. 30 mm	c. 53 mm	31 mm
5	—	10°	14 mm	55 mm	70 mm	35 mm
6	—	10°	12 mm	58 mm	70 mm	36 mm
7	30 mm	35°	11 mm	58 mm	70 mm	40 mm
8	33 mm	35°	—	59 mm	75 mm	41 mm
9	—	40°	10 mm	62 mm	75 mm	43 mm
10	30 mm	45°	—	62 mm	77 mm	39 mm
11	30 mm	40°	8 mm	64 mm	78 mm	41 mm
12	28 mm	40°	—	62 mm	78 mm	41 mm
13	25 mm	35°	7 mm	63 mm	78 mm	40 mm
14	25 mm	30°	—	64 mm	79 mm	45 mm
15	20 mm	25°	6 mm	65 mm	84 mm	43 mm
16	20 mm	30°	—	68 mm	88 mm	42 mm
17	20 mm	30°	4 mm	70 mm	91 mm	45 mm
18	20 mm	35°	—	70 mm	91 mm	42 mm
19	—	—	—	72 mm	94 mm	40 mm
20	—	—	—	74 mm	95 mm	44 mm
21	—	—	—	73 mm	93 mm	41 mm
22	—	—	—	74 mm	100 mm	41 mm
23	—	—	—	75 mm	100 mm	40 mm

THE INTERCENTRA OF PRESACRAL VERTEBRAE
(Figs. 1–4; 9 I; 10; 12; 13 A–C)

The dorsal intercentra are of the usual rhachitomous type, being crescents as seen in anterior and posterior view, convex side down. They are wedge-shaped in side view, apex upward. Concavities on their external surfaces may mark the paths of blood vessels. The inferior surfaces tend to descend as flanges anteriorly and posteriorly, least so in the posterior dorsals. A flat longitudinal ridge tends to develop mid-ventrally, best seen in the dorsal region. The surface may be notched posteriorly at the area of rib capitulum articulation. This is not well seen in young individuals and may be lacking in fairly large animals. It is most emphasized anteriorly in the presacral column, and at the sacrum (Fig. 12).

The anterior, posterior and dorsal surfaces are rough and unfinished, and presumably were continued in cartilage. The dorsal notch is a rounded longitudinal depression, occupied in life by the notochord and surrounding tissues. Four hummocks of bone, two fore and two aft, are arranged on either side of the depression and may represent centers of ossification (Fig. 13 A). These hummocks show with varying clarity, sometimes are completely obscured, and are illustrated as ridges by Broili (1899). Seen in side view the anterior pair of hummocks is slightly more ventral than the posterior in dorsal intercentra; the posterior hummocks are closer to the top of the intercentra.

Cartilage, with which the intercentrum was continuous, may have surrounded the notochord in life (Romer, 1947), but no ring intercentra have been found. Coossification of the pleurocentra occurs below the neural canal (Fig. 13 E), above the notochord (MCZ 2622 and 1652). Such a coossified piece may in turn coossify with the intercentrum to form a type of ring centrum in which all three elements are distinguishable (MCZ 2604 and 2562). A completely coossified vertebra has also been studied (FMNH UR745). Such remains are perhaps the best evidence of a vertebral column of ossified pieces embedded in a matrix of cartilage in *Eryops*.

Intercentra that were broken during life are rarely found. Two dorsal intercentra have been found (MCZ 2621, 4306; Fig. 13 B, C), which I think were so broken; a third (MCZ 4305) is cracked diagonally on the dorsal surface. Each break is at an angle clockwise to the anteroposterior axis (2621, 8°; 4306, 30°;

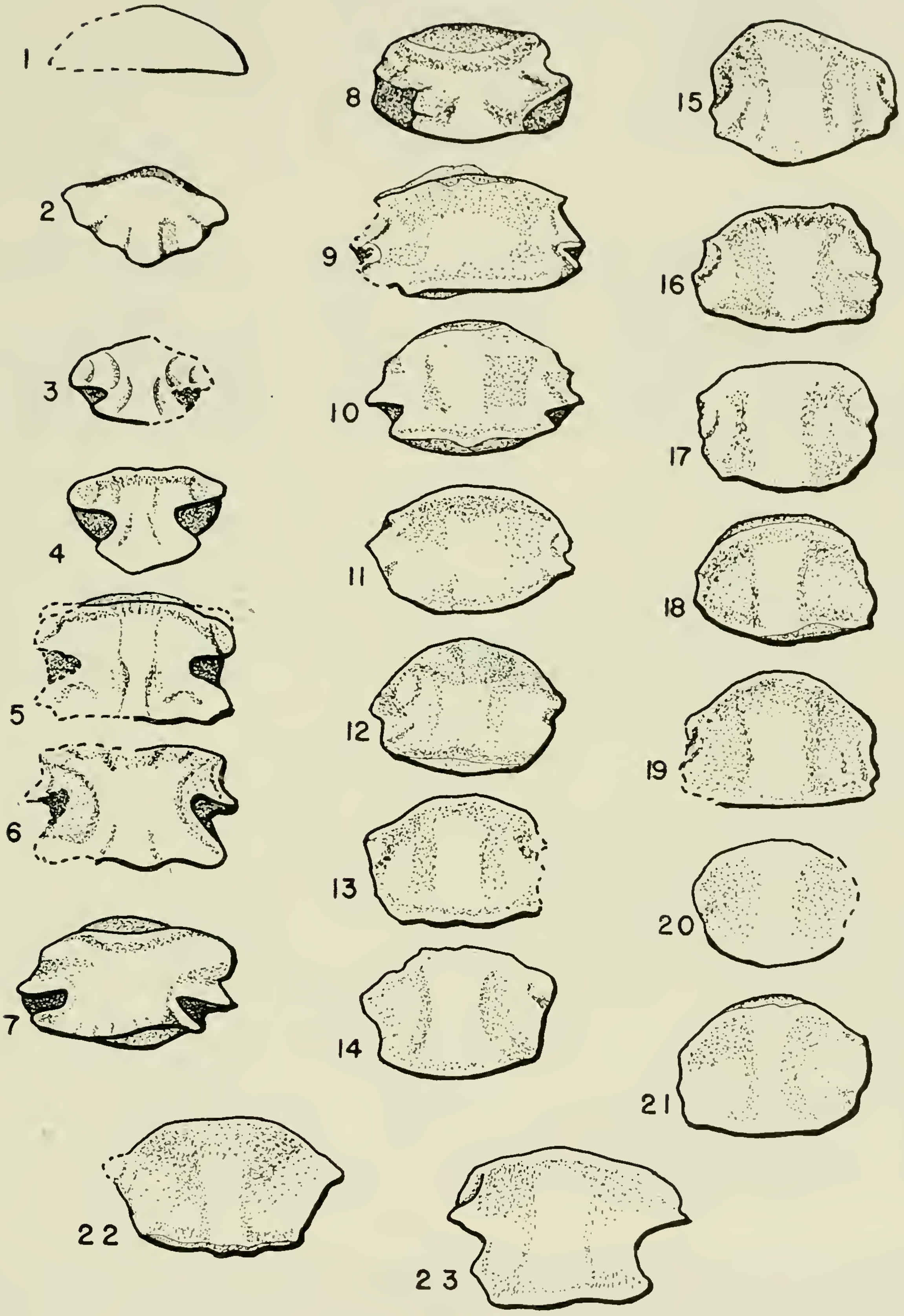
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Figure 12. The presacral and sacral (23) intercentra of *Eryops* in ventral view, anterior uppermost, × .6.

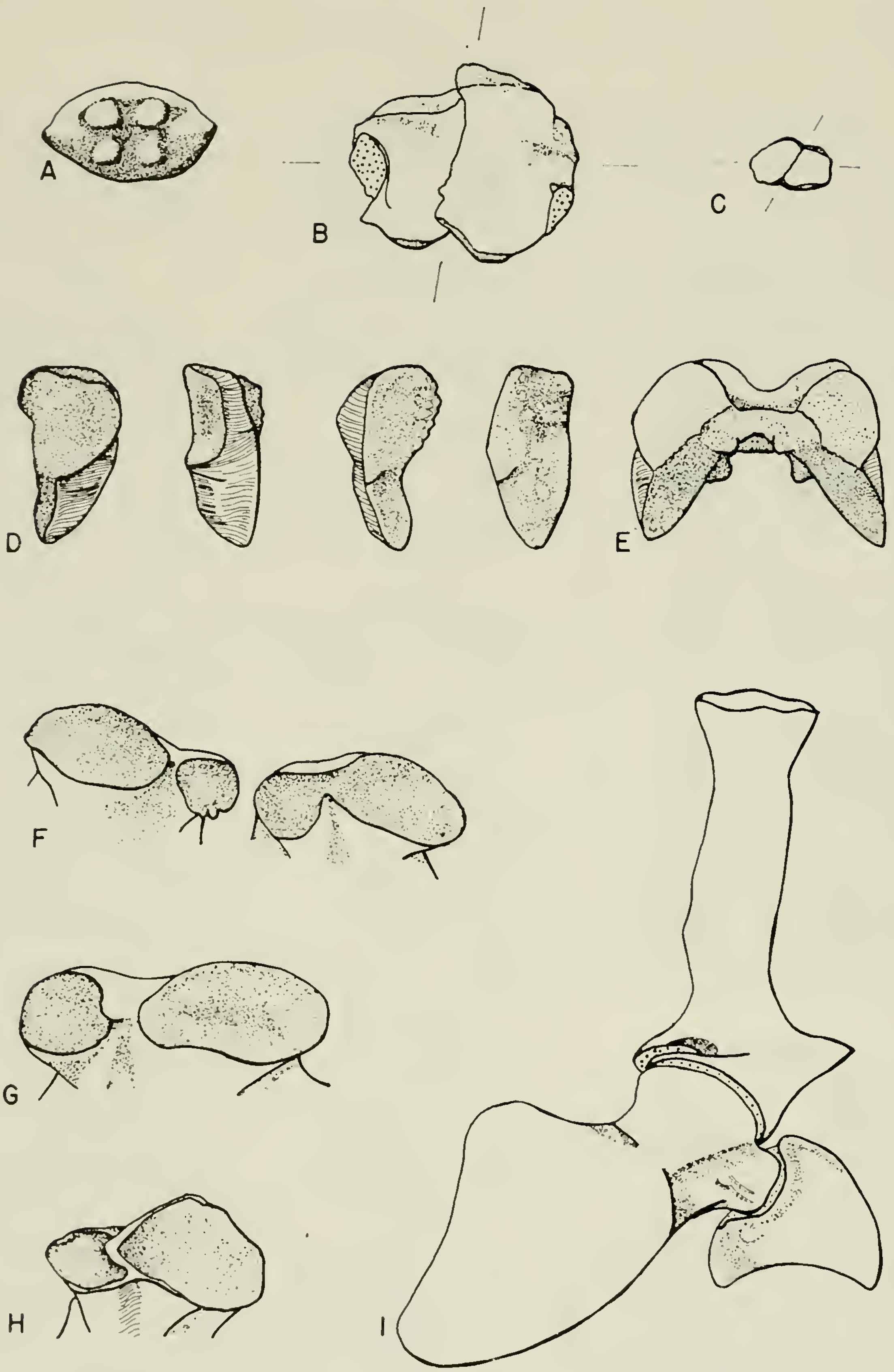

Figure 13. All × .5. (A) *Eryops* presacral intercentrum showing paired protuberances, anterior uppermost. (B) MCZ 2621, presacral intercentrum, ventral view, anterior at top, showing inclination of healed break. (C) MCZ 4306, intercentrum, as in (B). (D) MCZ 4307, a left pleurocentrum in anterior, lateral, posterior and medial views. (E) MCZ 2591, anterior view of coossified pleurocentra. (F) MCZ 4325, left and right sacral rib central articulations in ventromedial views. (G) MCZ 2085, right sacral rib central articulations in ventromedial view. (H) MCZ 2621, right sacral rib central articulations in ventromedial views. (I) Sacral vertebra and right sacral rib of *Eryops*, right view, pleurocentra not shown.

4305, 30°). That these breaks occurred in younger animals is evidenced by the small size of one intercentrum (MCZ 4306) and the appearance of extensive growth after healing in the other (MCZ 2621).

A fragment of the atlas intercentrum still clings to the left element of the atlas in AMNH 4183 (omitted by Cope and Matthew, 1915: pl. 12).

THE PLEUROCENTRA OF PRESACRAL VERTEBRAE

(Figs. 1–4; 9 I; 10; 13 D, E)

The pleurocentra are paired ossifications, the centers for which are situated dorsal to the notochord rather close to the midline. Study of articulations of components of the vertebrae indicate, however, that they must have been situated in pleurocentral cartilages of much larger size. Such cartilages would have appeared rhomboidal in side view, their longer sides articulating anterodorsally with the arch of the same vertebra, anteroventrally with their own intercentrum, posterodorsally with the next posterior neural arch, and posteroventrally with the next posterior intercentrum.

Their contours indicate that the ossified pleurocentral elements came close to the ventral margin of the column but did not reach it externally; restoration of the cartilage suggests that the cartilaginous pleurocentra probably did not gain contact with each other ventrally (Fig. 10 B). Dorsally, however, they were obviously in broad contact beneath the spinal cord; occasional coossifications in old specimens would suggest that the cartilages may have been continuous below the floor of the neural canal. The conjoined elements would have given in end view the appearance of an inverted crescent with the two horns closely approximated ventrally. The cartilaginous pleurocentra could have closely approximated those seen in ossified form in *Trimerorhachis.*

The paired centers of ossification of the pleurocentra appear to have been situated far dorsally where there is a globular mass of bone from which ossification proceeded slowly toward the ventral part of the element. The pleurocentra appear to be feebly ossified, and much of their surface area is unfinished in all but very old specimens. The more anterior pleurocentra are in general less ossified, and far anterior ones are almost unknown (see also Branson, 1905). A fifth pleurocentrum in the MCZ mount is finished on almost none of its surface, a fourth is a tiny nubbin on one side only and coossified with the arch, and there are no traces in material known to me of pleurocentra 1 and 2.

Exceptionally the two pleurocentra may abut medially, as they do in sacral vertebrae in two mature specimens (MCZ 2669 and 4305). There are cases in which the pleurocentrum has coossified with the neural arch, as on one side in two different sacra (MCZ 4305, 2604), and cases of coossification with the intercentrum behind (FMNH 60), or at one level with intercentrum and at another with neural arch (MCZ 1387), or with both in the same vertebra (FMNH UR745). Such cases are suggestive of a continuum of cartilage, the vertebral pieces embedded in it, similar to what Parrington has proposed.

The pleurocentra are likely to abut in the caudal region (MCZ 1787 and 2634), even to the point of occluding the notochordal canal (Fig. 15 F). The anterodorsal face of a pleurocentrum, that which articulates with the neural arch of its vertebra, is nearly flat and forms essentially a quadrant of a circle with a curved margin laterally and ventrally. In life this surface faced somewhat up and out as well as anterior and was apposed to the neural arch, although separated by at least a film of cartilage from it. The posterior surface is irregular, convex above, and apposed to but rather far from the anterior margin of the neural arch. The medial and posterior surfaces present a continuous, rough, curving form.

The external surface is in great measure finished. It is wedge-shaped in external view, narrow above, broadening and then tapering below. The margins curve up sharply anteriorly and posteriorly so that the pleurocentrum is externally concave in section; the curved margins are best defined above. The groove between the margins conveyed a spinal nerve. It narrows dorsally and at the very top turns anteriorly above the anterior articular surface to blend smoothly into the lower wall of the neural canal. The constant mismatch between the large surfaces on the neural arches for articulation with pleurocentra and corresponding anterior articular facets of the pleurocentra collected at the same time and place is a measure of the extent of cartilage beyond the borders of the ossified pleurocentra.

THE ATLAS–AXIS COMPLEX

(Figs. 1; 9 A–G; 14; Pl. I)

The neural arch of the atlas is highly specialized. The two sides may be separate (MCZ 1883) or coossified (AMNH 4183; Case, 1911). In the former case, each side consists of a stout pedicel and slender half arch and neural spine directed dorso-posteriorly. The pedicel is wedge-shaped with two broad articular surfaces, anteroventral and posteroventral. The anterior surface is for articulation with an exoccipital; the posterior is finished above (MCZ 1883), rough below where it articulated with the intercentrum of the axis. Each articular surface is a quadrant of a circle with a common straight ventral margin. The posterior surface is somewhat concave, not flat as usual. Internally there is a well-marked curved area for the side wall of the neural canal. At the base of the spine on each side is a flat tubercle, a well-defined anterior zygapophysis to seat the proatlas. Each half-spine is a thin rod, posteriorly and dorsally directed close to the axis spine. A tubercle or slight flange on the lower edge of the half-spine rested in life on the corresponding anterior zygapophysis of the axis.

The atlas intercentrum, seldom preserved, appears to ossify late. That associated with Sawin's (1941) specimen is a very flat crescent, with the outline of a slight notochordal space above, and the anterior edge with a central depression. There is only one pair of mounds, and the back surface is unexceptional. The front is subdivided into two articular areas facing rather laterally as well as anterodorsally, and obviously covered with much cartilage in life. The intercentra of atlas and axis have no capitular facets.

Each proatlas is a small neural arch, the short neural spine slanting back and upwards, its tip being irregularly rugose. At its base is an articular facet for the atlas tubercle. The anterior limb defines the upper edge of the foramen for the first spinal nerve and appears to barely touch the exoccipital region of the skull above and lateral to the foramen magnum; there is no formed facet.

There was undoubtedly restricted motion of the head, in the absence of a neck; the atlas-skull joint probably acted as a dorso-ventral hinge.

The axis neural arch is in many respects an ordinary one (Fig. 10). The neural spine is however elongated anteroposteriorly. The spine slants backward and then angles up in its longer dorsal portion, relative to a plane through the zygapophyses. The spine is wedge-shaped in frontal section, and is generally thicker posteriorly than anteriorly. There is a variable but gen-

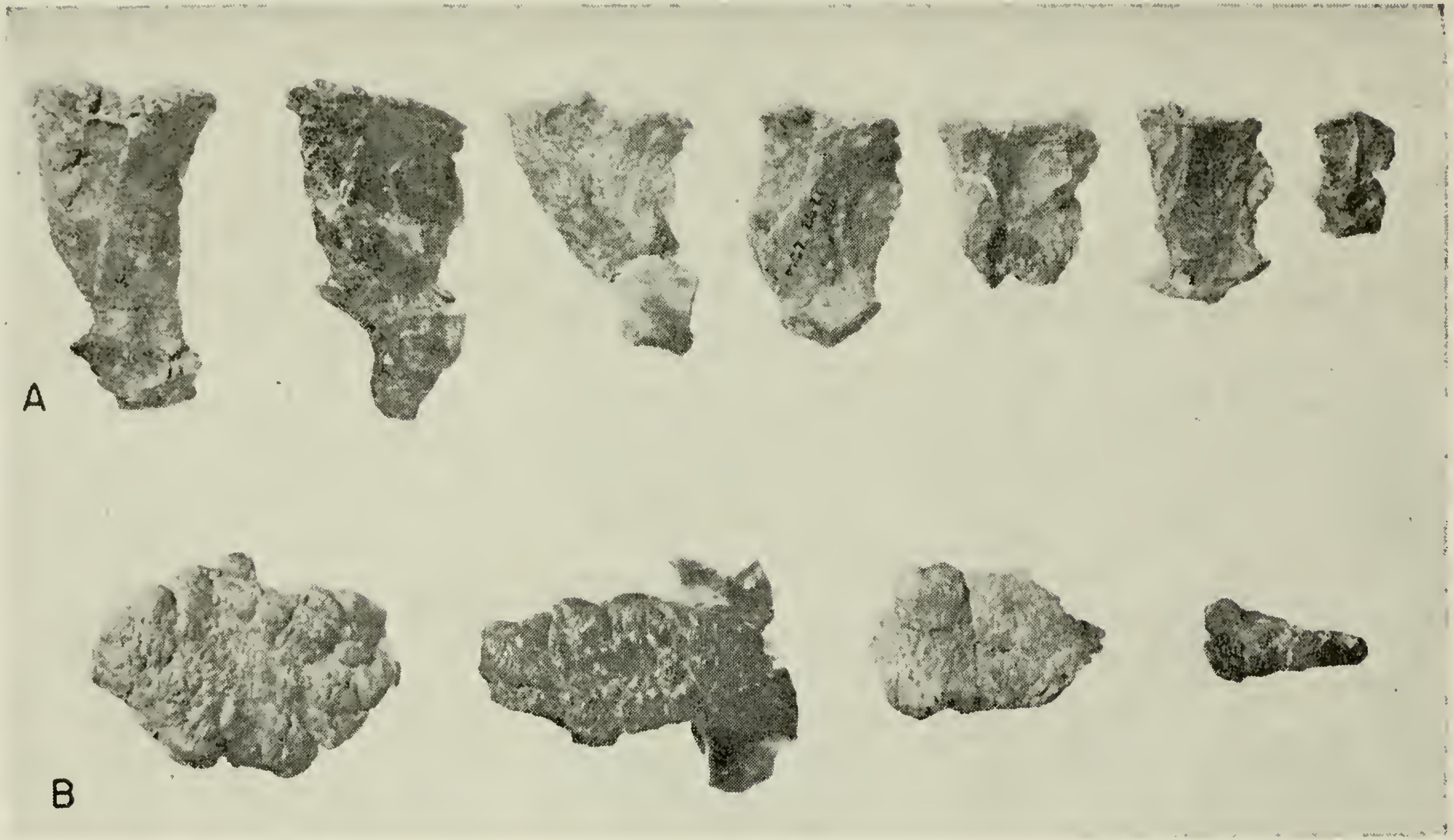

Figure 14. (A) Axis spines of *Eryops* cf. megacephalus, right lateral view. Left to right MCZ 2621, 1883, 3241, 2621, 3258, 4303; CMNH 11025 (*E. avinoffi*), × 5. (B) Dermal ornamentation of *Eryops* axial spines, anterior to right, dorsal views. L. to r. MCZ 2621, 1883, 2621; CMNH 11025, × .7.

erally prominent angle posteriorly, toward which a ridge is directed on either side from the widest point of the dorsal surface. Development at the front of the neural spine is very variable, depending in part on preservation. It is likely that a well-developed thin flange occurred on the front of the axis spine for a median ligament to the occiput. The anterior zygapophyses are much reduced to small flattened areas for articulation with the arch of the atlas. The pedicel and transverse processes are not specialized. The intercentrum of the axis is flat-bottomed, broad, and the posterior end has a rounded projecting keel. The axis is the most anterior vertebra to bear a rib. Constancy of form of the axis spine is illustrated in Figure 14 A.

VERTEBRA FOUR

(Figs. 1; 9 H; Pl. I)

This vertebra, with its specialized neural spine and anterior zygapophyses, makes up for restrictions in movement at the occiput. The posterior zygapophyses are normal, but the anterior ones are greatly expanded and nearly horizontal, thus permitting freedom of motion in the horizontal plane, together with some rotation vertically. The spine is much reduced (Case, 1911; Romer, 1943), a fact apparently not revealed by Cope's material. The spines of vertebrae 3 and 5 are inclined toward each other above that of 4; they are therefore distinctive. Their neural spines like that of the axis are somewhat elongate anteroposteriorly, and their facing edges are thinned, suggesting a special connection taking up the movement between vertebrae 3 and 4. These features are illustrated in Figure 1. In the Field Museum mount the spine of vertebra 4 curves slightly forward.

THE SACRUM

(Figs. 4; 10 F; 15 A; 12; 13 F–I)

The spine of the sacral vertebra is high and slants backward; in the MCZ mount the highest spine is that of vertebra 26, three behind the sacral (Table 2). The anterior zygapophyses are quite large, being the most posterior of an increasing size series. The posterior zygapophyses comprise approximately half the area of the anterior. The transverse process is enormously developed for articulation with the large tuberculum of the sacral rib, and the intercentrum bears a large facet for the capitulum. The facet may impinge upon the pleurocentrum (Fig. 15 A; FMNH

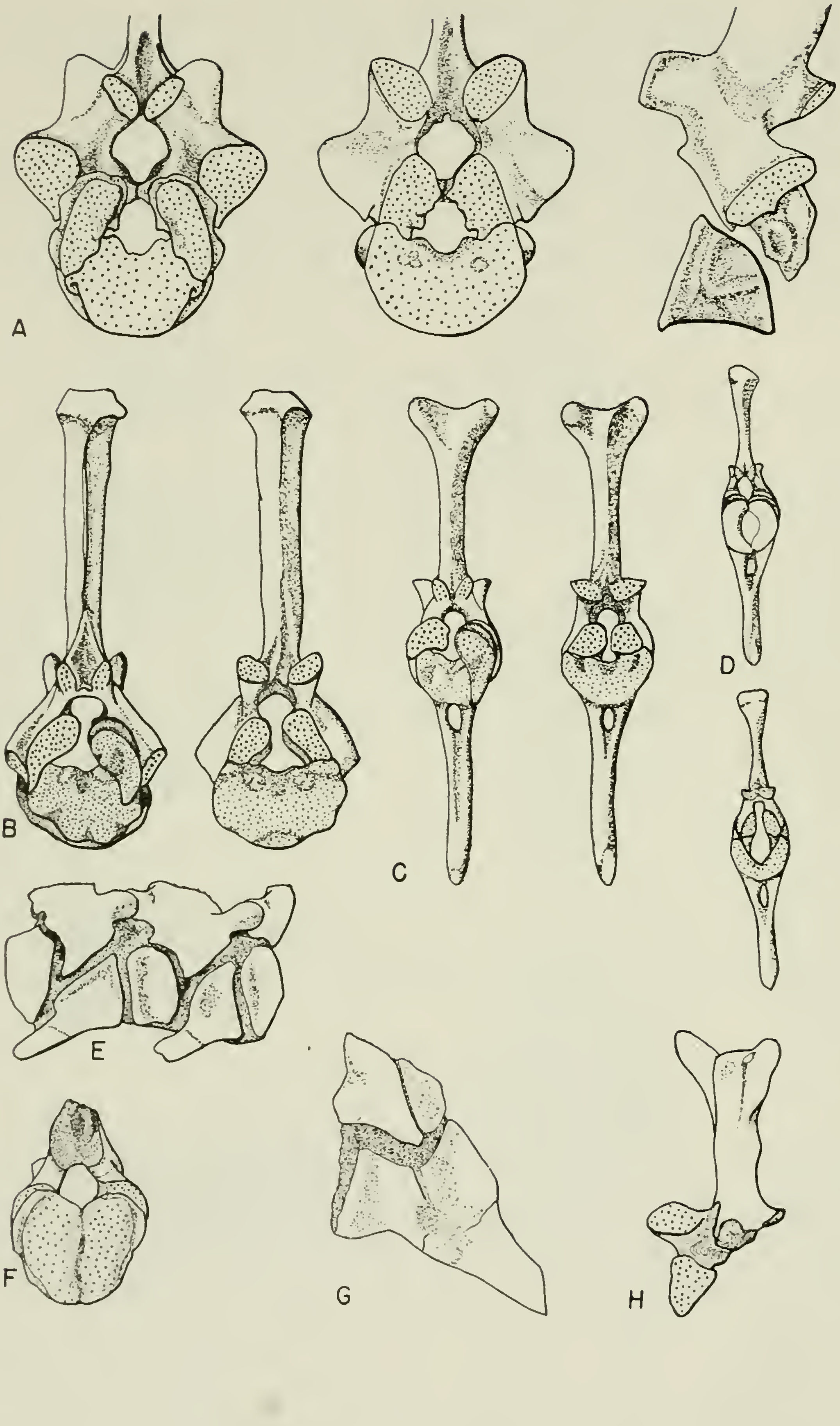
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Table 2. Some measurements of *Eryops* Anterior Caudal Vertebrae (MCZ 1539)

Vertebra	Height of Neural Spine	Greatest Length of Vertebra
1	75 mm	35 mm
2	78 mm	35 mm
3	80 mm	35 mm
4	73 mm	38 mm
5	71 mm	—
6	65 mm	36 mm
7	59 mm	—
8	59 mm	35 mm
9	52 mm	—
10	51 mm	35 mm
11	47 mm	31 mm
12	41 mm	31 mm
13	44 mm	—
14	38 mm	—
15	36 mm	29 mm
16	40 mm	—
17	39 mm	—
18	40 mm	—
19	33 mm	26 mm
20	33 mm	—

←

Figure 15. All × .5. (A) *Eryops* sacral vertebra (23), spine omitted, in posterior (l.), anterior and left views, the latter of MCZ 4305. (B) *Eryops* vertebra 27 (caudal 4), posterior (l.) and anterior views. (C) *Eryops* vertebra 33 (caudal 10), posterior (l.) and anterior views. (D) *Eryops* vertebra 43 (caudal 20), posterior (above) and anterior views. (E) MCZ 2634, right view, showing matrix (dark stippling) occupying position postulated for cartilage about centra of postsacral vetebrae. (F) MCZ 1787, posterior view, spine missing, showing closure of notochordal canal by pleurocentra. (G) AMNH 4183, left view, showing fusion of two successive chevrons. (H) MCZ 4325, left lateroanterior view of one to three caudal vertebrae showing perforation of dorsal expansion of neural spine on the left side for segmental blood vessel.

UC60 and UC117), this being a characteristic of old and of very large specimens. The sacral rib may fuse to or coossify with its central articulations (FMNH UC117). The coossification of elements is not uncommon at the sacral vertebra, although the degree of fusion may differ on the two sides (MCZ 4305, 2669, 2604).

THE CAUDAL VERTEBRAE

(Figs. 5–8; 15 B–H; 11; the measurements in Table 2)

The total number of caudal vertebrae in *Eryops* is about 40. The number of vertebrae may vary, but the possession of ribs on the first eight caudals with chevrons beginning on the eighth vertebra is taken as typical. The proximal caudal neural arches are closely comparable to the presacral ones in their general features, with less anteroposterior extension at the top, and with the zygapophyses placed more closely together. In the trunk region, the shaft of the neural spine tends to curve back and then up, whereas in the caudal the longer part reaches upward before the backward bend, this curvature being more pronounced posteriorly. The heights of the caudal spines gradually decrease and the tops change from an oval outline and become bifurcated, at about caudal 4, into two abbreviated horns with rounded summits, one on each side, directed first posterolaterally (4–10), then laterally (11, 12), and then anterolaterally (13–20). Behind caudal 20, bifurcation is not noticeable. The horns are not always symmetrical; one may be anterior to the other. They were covered by skin in life (Romer and Witter, 1941). Near vertebrae 20 to 22, the neural spine tips are altered, becoming single again. By this point, the spine is much shortened with a strong back-and-up curve, is thin from side to side, and is rather long anteroposteriorly.

The zygapophyses are closer together and more sharply tilted than in the dorsal vertebrae, and there is a reduction in size. In the first dozen caudals, the sides of the neural arch tend to be somewhat concave between the zygapophyses, as in the dorsal vertebrae. After that they are quite flat. In the MCZ mount transverse processes with broad but thin ends that gradually narrow occur on the first seven caudals and exceptionally on one side of the eighth. Behind the eighth, the pedicels are smooth, although convex and swollen along their posterior borders. Each vertebra, and hence its pedicels, becomes relatively and increasingly narrow in the tail, so that the sides of the pedicels are more vertical. The surfaces facing the pleurocentra and intercentrum are similar to those in the trunk for most of the length. In old specimens, the floor of the neural canal may be complete (Fig. 11), suggesting that cartilage extended through the area in younger specimens. The pedicels narrow below the spinal nerve foramina.

In the proximal part of the caudal column, each pleurocentrum tends to broaden at the top, flatten on the lateral surface, and extend relatively far down. They tend to become relatively large and more important, and distally may approach the embolomerous ring type (MCZ 2634). In the sacral region especially, the two bony pleurocentra become closely approximated dorsally, and the ventral ends tend to approach one another more closely than elsewhere. It is possible that in mature specimens they fused into a ring, but no such specimens have been seen, although intercentrum and pleurocentra together may coossify into a ring centrum. Pleurocentrum enlargement and coossification of vertebral elements in the sacral region may be adaptations for terrestrial life.

In the MCZ mount, the first seven intercentra of the tail lack a haemal arch; the first chevron is on the right side of vertebra 8, the left side presenting a transverse process and rib. This count may have varied depending on the extent of the coelom in the cloacal region. The proximal intercentra are like those of the trunk, but capitular facets are well marked and the intercentra are more convex ventrally than dorsal intercentra. A medial ventral groove appears in intercentrum 7 for the caudal blood vessel which posterior to vertebra 7 courses through the foramina of the haemal arches. These arches tend to develop a keel on the front and to be flat behind, and to develop small terminal cartilages. The shafts gradually become shorter, the foramina occupying a progressively greater extent of their length. Distally, the ends become flattened and tend to become anteroposteriorly oriented, shoe-shaped expansions.

To a greater or lesser extent, the neural spines of *Eryops* vertebrae show lateral grooves where segmental blood vessels have coursed. On each of three caudal vertebrae of MCZ 4325, near the front of the bifurcated spine series, a shallow groove appears on the left side of the neural spine perforating or indenting the dorsal tuberosity of the neural spine (Fig. 15 H). These three are unique in the collections I have studied; presumably all came from the same animal.

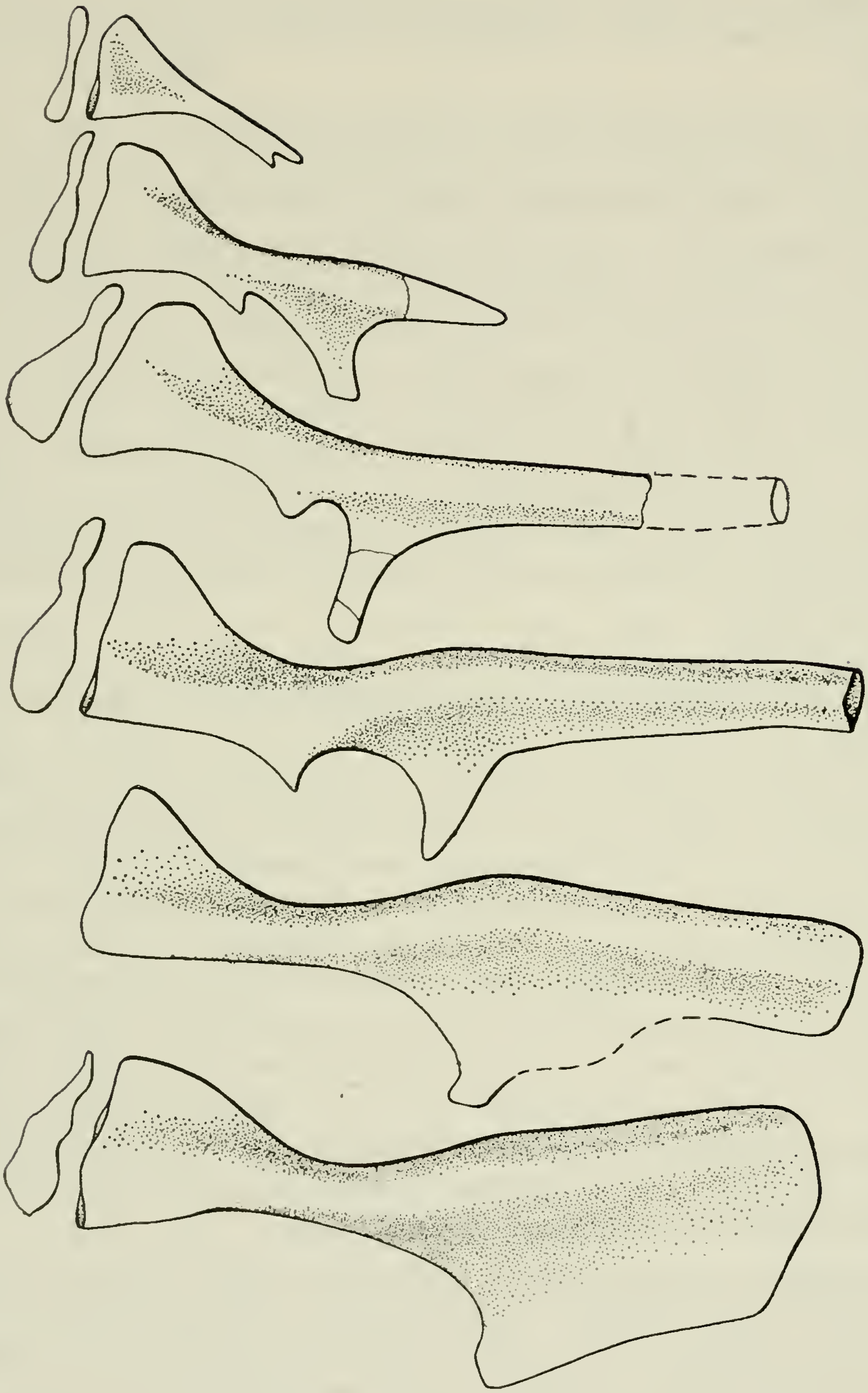

Figure 16. *Eryops* right presacral ribs 1–6 (of vertebrae 2–7) with outlines of articular surfaces above; × .5.

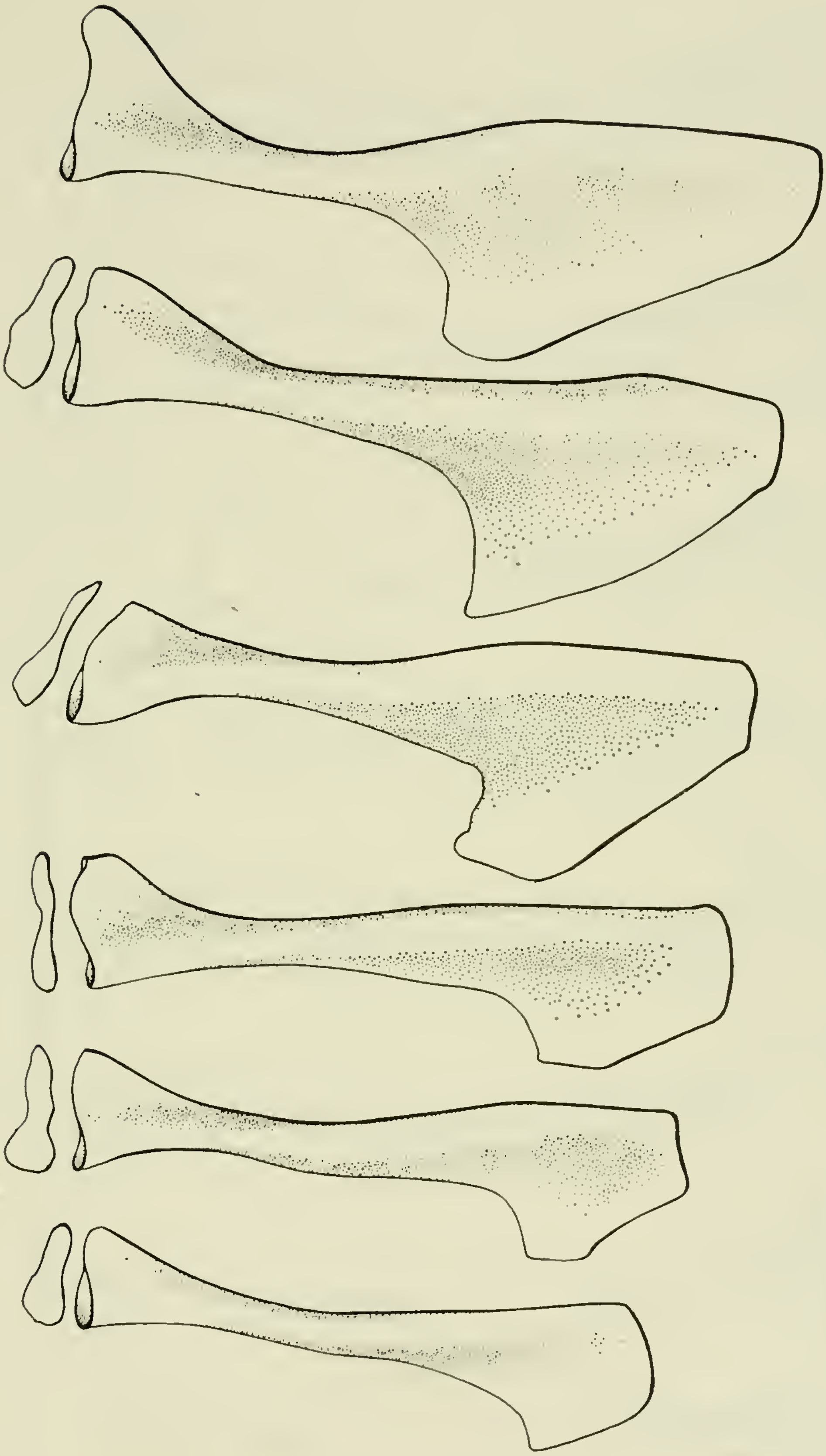

Figure 17. *Eryops* right presacral ribs 7–12 (of vertebrae 8–13), × .5.

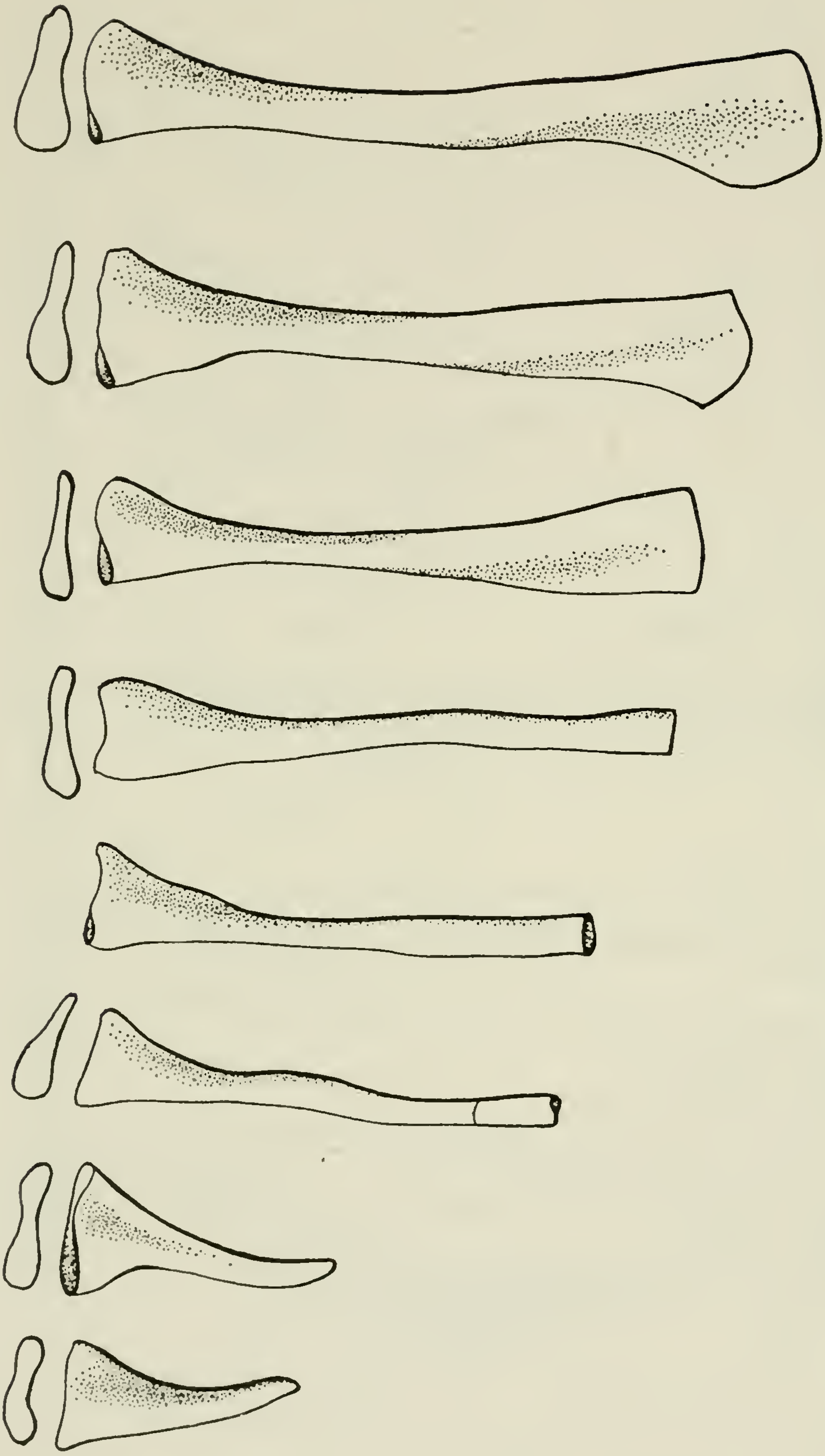

Figure 18. *Eryops* right presacral ribs 13–20 (of vertebrae 14–21), × .7.

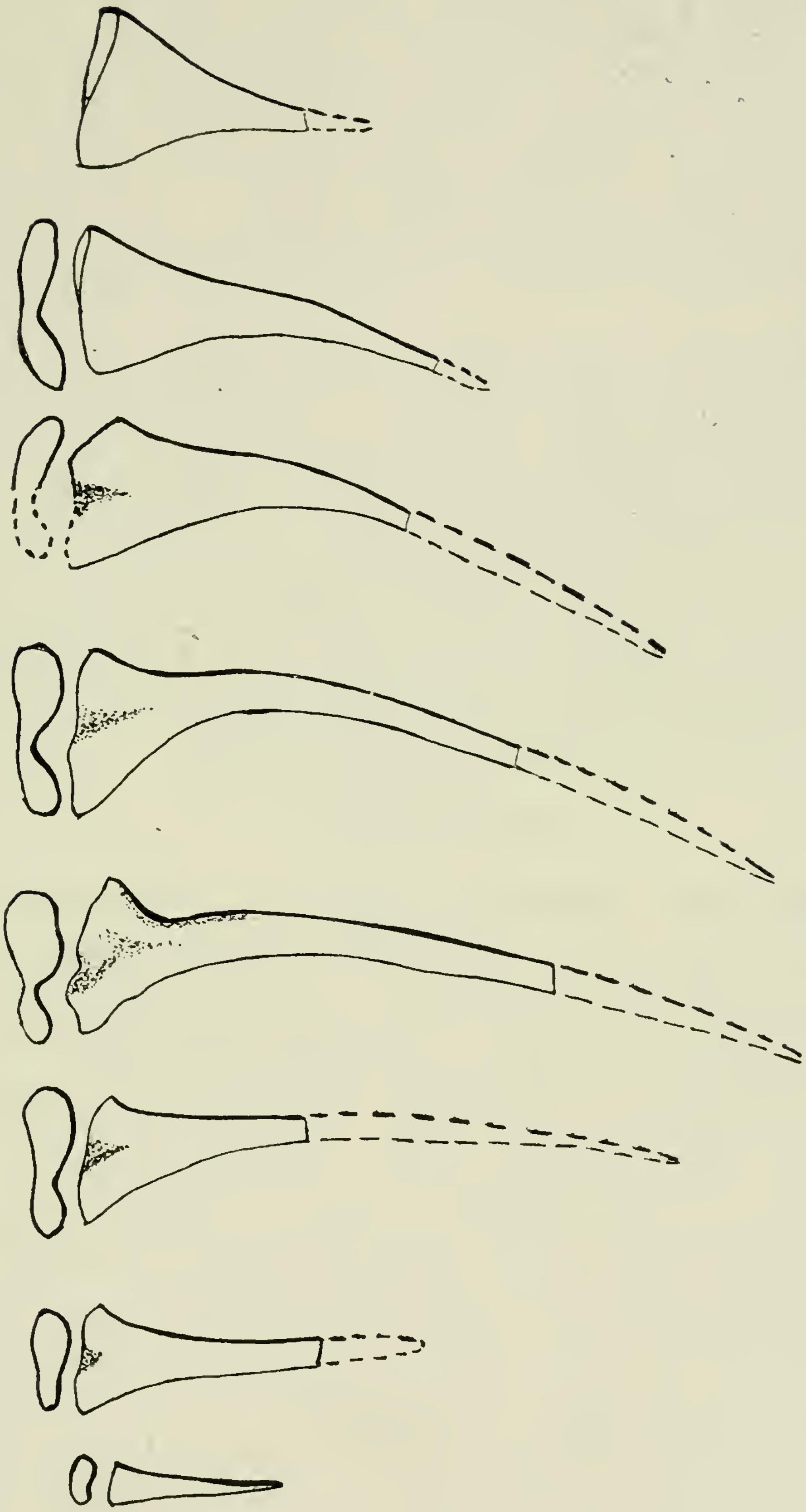

Figure 19. *Eryops* right postsacral ribs 1–8 (of vertebrae 24–31), × .7.

THE RIBS

(Figs. 13 F–I; 16–19)

Of the 22 presacral vertebrae, the first (atlas) lacks a rib; in some mounts the last presacral rib, that of vertebra 22 has been omitted, while in others a misplaced ilium spans too many ribs. The head of all presacral ribs is expanded, with only a constriction separating capitulum and tuberculum. The tubercular part is somewhat thicker than the capitular. The articular surfaces are somewhat concave and unfinished, suggesting a cartilaginous surface coat. The proximal rib ends are inclined clockwise from the vertical, as are the corresponding articular surfaces of the transverse processes (Table 1). The ribs are flat distally. There are thickenings of the shaft continuous with capitulum and tuberculum, and there may have been considerable variation in the form of the uncinate processes. The distal rib ends are unfinished, except those of the posterior presacrals, and presumably ended in cartilage, but this is uncertain. In the MCZ mount, uncinate processes are shown on the 2nd through the 13th ribs, reducing in size and disappearing as the ribs shorten posteriorly. Caudal ribs lack these structures.

DISCUSSION

It is clear that — distortion apart — individuals of *Eryops* were variable in the following details of their spinal columns: extra processes and exostoses; closure of neural canal; degree of definition of capitular facets; relative sizes of neural arches, intercentra and pleurocentra; degree and asymmetry of coossification; shapes of neural spines and of atlas, axis and the special fourth vertebra; angles of inclination of the neural spines, and details of configuration of their dorsal expansions. Nevertheless, a clear picture emerges of a repeated series of ventral intercentra, dorsal neural arches and paired dorsolateral pleurocentra probably separated or held together in life by cartilage, which may have been continuously woven among the centra or interrupted between vertebrae anterior to each intercentrum; it is not clear from the fossil record which was the case. Presumably cartilage was more extensive in younger than in older animals. The unfinished articular surfaces of vertebral elements clearly reflect their continuation in cartilage.

Arrangement of vertebral elements varies considerably in existing *Eryops* reconstructions. Fossilized pieces, even when found adjacent, are, unless coossified, often difficult to fit exactly to each other, presumably due to the missing cartilage. We have found no reason to quarrel with Cope's (1890) description, which is an excellent guide to vertebral arrangement in *Eryops:* "The neural arch rests exclusively on the pleurocentrum, which in turn adheres to the intercentrum behind it by its long side, and to that in front by its short side or end", and of caudal vertebrae ". . . the pleurocentra descend further than in the dorsal region, rarely to the inferior face of the column, and separating the intercentra from mutual contact." These points are illustrated in Figures 10 and 15.

As regards the function of the rhachitomous vertebral column, two views have been advanced. Cope (1884) proposed a coat sleeve on a semiflexed arm as a model of the flexible cylinder to which he earlier (1883) had likened the column of *Eryops.* He saw the osseous elements of the rhachitomous vertebral column distributed through a sheath of softer tissue around the notochord, like segments of the skin of an orange — segments of a sphere, as it were. "If you take a flexible cylinder, and cover it with a more or less inflexible skin or sheath, and bend that cylinder sidewise, you of course will find that the fractures of that part of the surface will take place along the line of the shortest curve, which is on the side; and, as a matter of fact, you have breaks of very much the character of the segments of the Permian batrachia" (1883: 276). In a coat sleeve covering the semiflexed arm, the folds represented to Cope the fractures in the flexible cylinder, the intervals between elements, and the spaces between folds the elements themselves. Cope left it to future investigations to determine the applicability of his model to the history of the vertebral column (1884: 32).

Parrington (1967) suggested a geodetic spiral, presenting the rhachitomous vertebral column as a series of discrete ossicles in a cartilage continuum, allowed to twist by virtue of the embedding of the rather rhomboidal osseous elements interdigitated in a cartilage matrix. Such twisting, Parrington suggested, would have been essential for amphibious tetrapods like labyrinthodonts on coming ashore in order to maintain a center of gravity upon a triangle of three legs while bringing the fourth leg forward for the next step. Coalescence of neural arches and neural spines in certain armored rhachitomes has led Vaughn (1971) to question whether or not Parrington's model can have applied to locomotion in these particular labyrinthodonts. On the other hand, the flexibility in vertebral column which Parrington's model provides would, it seems to me, lend itself ideally to the stereotyped locomotion probably imposed upon a large, tailed amphibian such as *Eryops* by extension of the supracoracoideus muscle, between coracoid and humerus, to the forearm through the coraco-radialis proprius, as I have discussed it for living urodeles (Moulton, 1952). While the arrangement may have relieved *Eryops* from decisions leading to more complicated locomotory patterns, the simultaneous adduction of the forelimb and flexing of the forearm, re-establishing at each step the triangle of three legs as envisoned by Parrington, would have abetted the twisting of a spirally organized vertebral column and vice-versa. It is noted that Miner (1925) questions the occurrence of the coraco-radialis proprius in *Eryops*. Thomson and Bossy have argued (1970) that the temnospondyl and anthrocosaur amphibian lineages represented different experiments in a terrestrial vertebral column, both based on the principle of a geodetic spiral enunciated by Parrington.

The spiral pattern suggested by Parrington seems reasonable as a device for strengthening a vertebral column like that of *Eryops* subject to the stresses of locomotion on land. Are there evidences of the proposed torsion in fossil material? I believe so. Two intercentra broken and healed during life (MCZ 2621, 4306), and one that developed a shallow dorsal split also during life (MCZ 4305) have been encountered (p. 22). Inasmuch as each occurred at an angle clockwise from the primary axis (MCZ 2621, 8°; 4306, 30°; 4305, 30°), I suggest that these breaks may have occurred in young animals and that they may reflect the twisting hypothesized by Parrington in his spiral model. Such breaks are not common in fossil collections, the ones described being unique among the intercentra I have studied.

At present, the detailed pattern of evolution of vertebral centra is unsettled. Recent papers of special significance are those of Williams (1959), Panchen (1967), Thomson and Vaughn (1968) and Thomson and Bossy (1970). Despite gaps in our knowledge of the details, there is a general concensus that some form of the rhachitomous vertebra was the primitive amphibian type; however, increasing evidences of variation in vertebral pattern among primitive amphibians greatly complicate the picture (R. L. Carroll, personal communication). *Eryops* itself has moved along the temnospondylous line from the most primitive labyrinthodont condition (Romer, 1947). In suggesting that the amphibian centrum is homologous throughout, but differently subdivided in different lineages, Panchen (1967) introduced an idea open to examination by determining the attachments of myosepta to the vertebrae, for in all tetrapods, it is clear since the important review by Williams (1959), caudal and cranial half sclerotomes of successive somites unite, resulting in alternation of vertebrae and primary muscle segments. Panchen saw the vertebral margin of the myoseptum with its segmental blood vessel providing the dividing line between intercentrum and pleurocentrum. In temnospondyls he saw the myoseptum moving posterodorsally, ultimately to the stereospondyl condition, leaving an increasingly large intercentrum ahead of the myoseptum until the pleurocentrum disappeared. Anteroventral movement of the myoseptum on the anthrocosaur line would have resulted ultimately in the loss of the intercentrum, and in an amniote centrum formed from the pleurocentrum posterior to the myoseptum.

While I have no new evidence on the course of the intersegmental blood vessels in relation to the centra in labyrinthodonts, the pathway for the blood vessels and myosepta postulated by Panchen (1967: 28) as applicable to fossil material is supported by the three neural arches of caudal vertebrae (p. 33) which are grooved and perforated on the left side almost certainly for the passage of segmental blood vessels. A similar pathway on dorsal vertebrae of *Eryops* could easily have been continued along the tops of the transverse processes (p. 20), behind the well-defined ridge already described, then dropping behind the rib blades almost exactly as Panchen describes and illustrates (1967: fig. 5A). Since the courses of segmental blood vessels have rarely been preserved in labyrinthodont vertebrae (Panchen, 1967: 28), these three clearly marked caudal vertebrae assume a special significance to our understanding of vertebrae and muscle segments in *Eryops*.

The broadly flat form and orientation of most of the trunk ribs in *Eryops* probably did not allow for much lateral undulation, such as suggested by Thomson and Bossy (1970: 11) for *Ichthyostega*. The tail, however, would have served as an excellent swimming organ; reconstructions that show it as flexible and leaning toward one side on land may be close to the truth. That it was strengthened by dorsal tendons seems likely from the bifurcate nature of some of the spines.

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ANOLIS RUPINAE NEW SPECIES A SYNTOPIC SIBLING OF A. MONTICOLA SHREVE

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and

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Abstract. A new species, *Anolis rupinae,* is distinguished from sibling *A. monticola* by its larger size and different coloration. These two species and *A. koopmani,* which is smaller than either and somewhat different in coloration, scale characters, and habitus, constitute a subgroup in the larger *monticola* species group. All three occur on the western end of the Tiburon Peninsula of Haiti and have karyotypes derived by fission of one or more macrochromosomes from the primitive iguanid complement. The remaining four species of the *monticola* species group are morphologically more diverse and occur north of the Cul de Sac depression. Three have the primitive karyotype. *Anolis rupinae* is known only within the habitat of *A. monticola,* but is allotopic to *A. koopmani.* Chromosome change may have been important in the evolution of this distinctive miniradiation.

As Schwartz (1973) has commented, it is clear that the roster of Hispaniolan *Anolis* species is not yet complete. Webster and Burns (1973) have just demonstrated that the *A. brevirostris* complex in Haiti must be divided into three species, and Schwartz (1973, 1974a) has described two striking new species in the Dominican Republic. In addition Schwartz (1974b) has shown that the Hispaniolan giant anoles heretofore considered a single species, *A. ricordi,* are better interpreted as three species.

The key feature of all the recently described Hispaniolan anoles is that they are *local* species. They may or may not be abundant where they occur but they all have restricted distributions, often montane, sometimes in very arid regions, often less

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obviously circumscribed. Sometimes they are known from a single locality, more often from a number of localities relatively close together. The species of the *ricordi* complex have the widest ranges of any of the newly recognized forms, but again these are allopatric or parapatric, none islandwide.

We here add still another local species, the major peculiarity of which is that it is syntopic with its closest relative.

Anolis rupinae[1] new species

Holotype. MCZ 121740, an adult male.

Type locality. 1.3 km SSW Castillon, Departement du Sud, Haiti, T. P. Webster and A. R. Kiester, collectors, 6 September 1969.

Paratypes. All Departement du Sud. From the type locality: MCZ 121737–39, same data as the type: MCZ 124475–87, 124612–15, 124851, T. P. Webster collector, 2 July 1970.

Diagnosis. Close in all scale characters and counts to *Anolis monticola* but differing in larger size and in color.

Head. Head moderate, head scales rugose or keeled. 9 to 15 scales across snout between second canthals. Frontal depression shallow, scales within it as large or larger than those anterior and lateral to it. Anterior and ventral nasal scales (or these plus the anteriormost of the lowest loreal row) in contact with rostral. 7 to 11 scales in contact with rostral posteriorly. Supraorbital semicircles separated by two rows of scales. 10 to 17 keeled scales in supraocular disk, which is separated from the supraciliaries by five or more rows of granules. Two elongate supraciliaries ending at about mid-eye, continued by granules. Canthals distinct; about 6 to 7 canthals, the first three elongate, strongly overlapping, first sometimes as long as second. Loreal rows 6 to 9, lower row slightly larger, supratemporal rows slightly enlarged. Temporals granular, scales behind interparietal very slightly enlarged, those anterior and lateral to it markedly larger. Interparietal smaller than ear, separated from supraorbital semicircles by 3 to 6 scales. Suboculars separated from supralabials by one row of scales. Six supralabials to center of eye. Lower eyelid with a window of granular scales.

Mental much broader than long, in contact with 4 to 8 scales between the large sublabials. Only one or two sublabials on each side clearly defined, posterior to these there are two to three rows

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[1] from the Latin *rupina:* a rocky chasm.

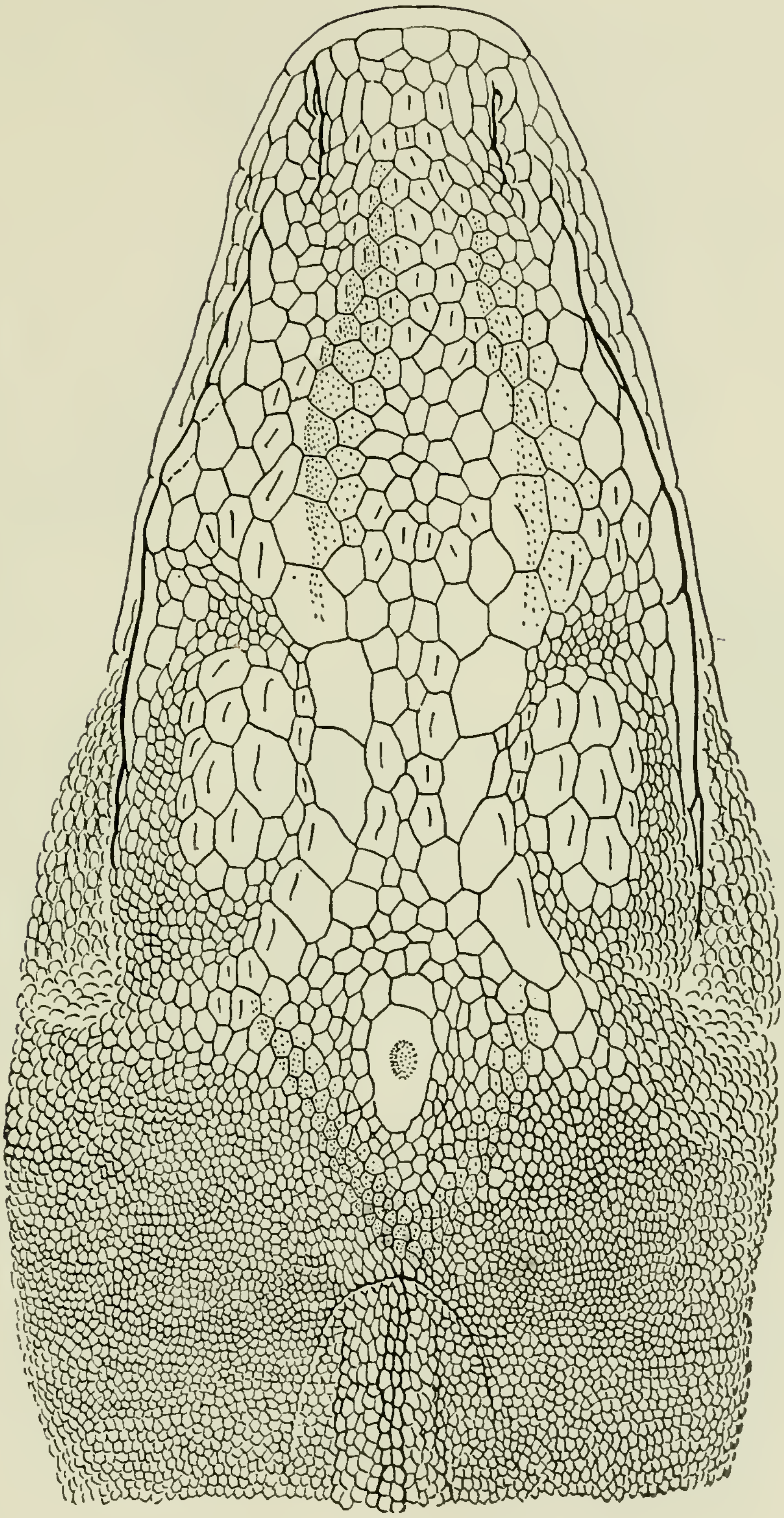


Figure 1. *Anolis rupinae*, MCZ 124857. Dorsal view of head.

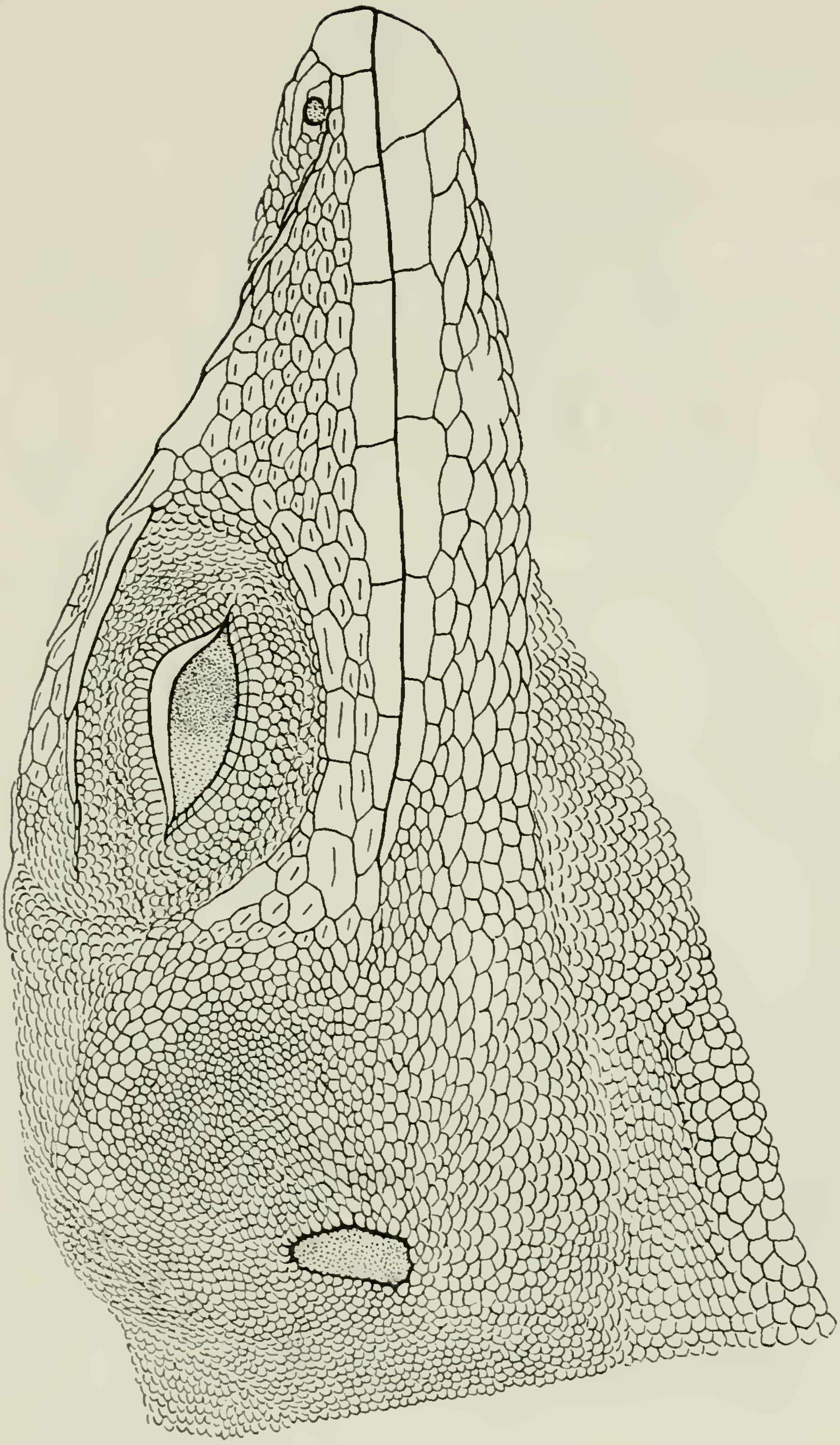


Figure 2. *Anolis rupinae*, MCZ 124857. Lateral view of head.

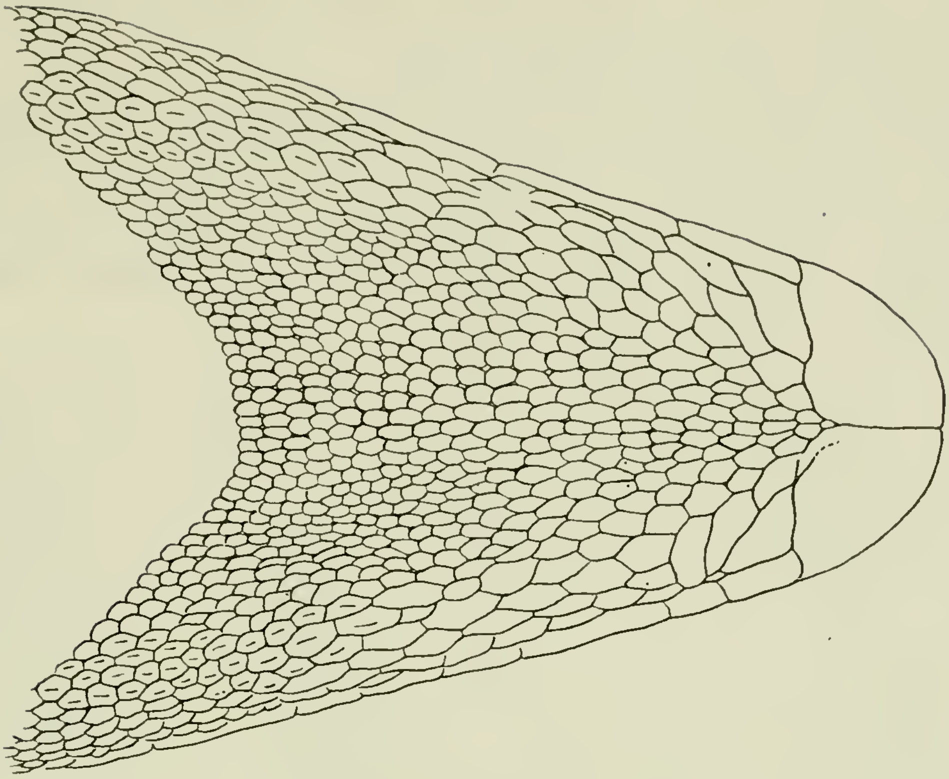


Figure 3. *Anolis rupinae,* MCZ 124857. Ventral view of chin.

of enlarged scales alongside the narrow infralabials. Throat scales smaller, slightly elongate anteriorly.

Trunk. Two to three middorsal scale rows enlarged, keeled. Flank granules keeled. Ventrals larger than middorsals, weakly keeled, imbricate, subimbricate or rarely juxtaposed.

Dewlap. Small, in males only but extending to the level of the axillae, the largest scales about as large as ventrals, weakly keeled.

Limbs and digits. Dorsal scales of arm and anterior scales of thigh and of lower leg unicarinate. Those of digits and of knee multicarinate. 16 to 21 lamellae under phalanges ii and iii of fourth toe.

Tail. Compressed, four middorsal scales per verticil. Postanal scales large in male.

Size. Males to 56 mm in snout-vent length, females to 42 mm.

Color in life. Webster, 6 September 1969: Adult male type from Castillon: "Snout uniform olive green above. Neck subtly mottled with shades of olive and pale green. Five pale green transverse bands from neck to base of tail. Middorsally the nuchal and dorsal crests have alternating areas of pale blue-green and olive. More laterally the transverse bands separate olive brown blotches with yellowish spots in them. Dorsum of base of tail with areas of olive alternating with pale green. Distally, tail black alternating with greenish cream.

"Side of snout pale dull green. Eyelids yellow-orange. Iris turquoise. Pupil black. Behind eye very dark green. Below it pale green. From shoulder along flank a bright green stripe, broadening where it crosses the transverse bands, which are lighter green on the lower flanks.

"Below, chin pure bright yellow. Dewlap scales yellow. Skin sky blue. Chest scales yellow, those of belly not so bright and with the yellow intermingled with areas of dull orange. Under tail red orange spots surrounded by yellow scales, the spots becoming more diffuse and vanishing toward the tip.

"Limbs dorsally with alternating light yellow green and light brown. Two green bars on upper and lower arm and tibia but three such bars on the femur. Hand and foot similarly crossbarred. Ventrally, limbs mottled yellow brown."

Webster, 1 July 1970 (Castillon): "All sizes and both sexes of *rupinae* can be distinguished from *monticola* by the red-orange color on the ventral surface. Males are larger, lack the scapular patch and have a blue (sky blue) dewlap and a brilliant green lateral stripe. The edges of the middorsal band in females are straight without scalloping. In both sexes bright yellow around the eye."

Color as preserved. The green stripe so conspicuous in life is usually absent in preserved specimens. The red of the ventral surfaces also vanishes and the dorsal banding is less vivid. In preserved male *rupinae* the most marked difference from *A. monticola* is the absence of any scapular spot. Females are more difficult but the red spots under the base of the tail in life are seen in preserved specimens as very white spots which may coalesce to an undulating bright line under the first part of the tail. (In *monticola* light pigment under the tail is weakly developed or present as a straight-edged line.)

Karyotype. Diploid chromosome numbers are known for two male paratypes (MCZ 124612–13). In diakinesis one has five macrochromosomal bivalents and one trivalent, while the other has six bivalents and one trivalent. Both have 13 small bodies interpreted as microchromosomal bivalents. On the basis of this minimal sampling of the one known population, diploid numbers in *A. rupinae* should vary from 38 to 42.

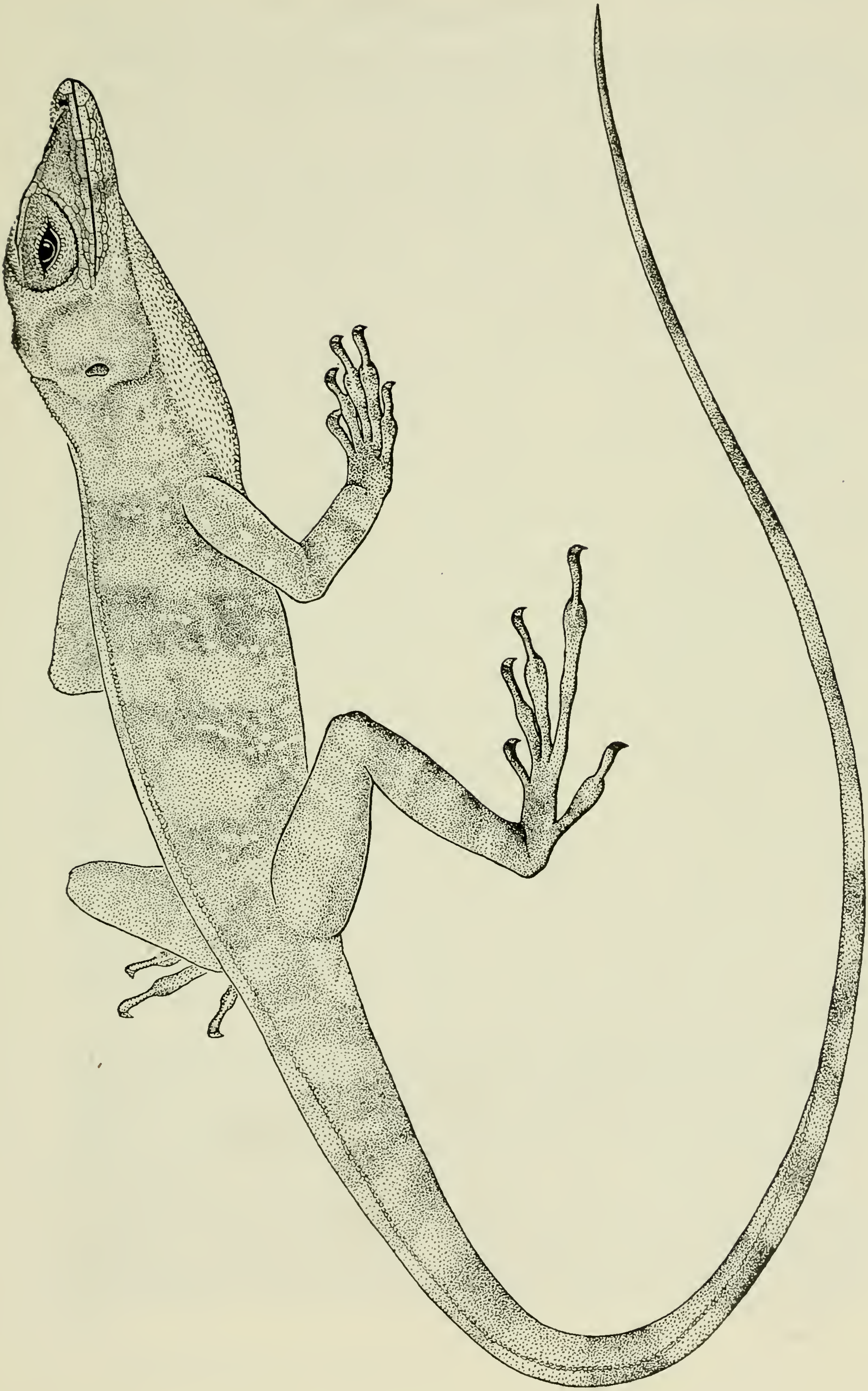


Figure 4. *Anolis rupinae*, MCZ 124857. Lateral view to show pattern in preserved specimen.

COMPARISONS

A. rupinae requires comparison only with certain members of the *monticola* group, and only nominate *monticola* is known to co-occur with it.

In scale characters *rupinae* (Table 1) is either identical with *monticola* or (as the snout scales) overlapping. However, though both are richly, even gaudily colored, the two species are sharply distinct in color (Table 2). The bright flank stripe of *rupinae* is missing in *monticola* while the two (nuchal) or four (nuchal and occipital) black patches with blue ocelli of *monticola monticola* and *monticola quadrisartus* are absent in *rupinae*.

In dewlaps, although small in both species, there is a contrast also. At the Castillon ravine, *monticola* has a yellow to reddish orange dewlap while that of syntopic *rupinae* is sky blue.

Adult size also distinguishes *A. rupinae* from syntopic *A. monticola*. However, on this point there is a confusion in the literature. Thomas and Schwartz (1967) cite the maximum size of *monticola* males as 55 mm (they do not mention the specimen) and that of females as 39 mm. They comment on the strong sexual dimorphism. We have at hand Thomas Schoener's measurements for specimens referred to *monticola* in Schwartz's collection, the earlier collections of the Museum of Comparative Zoology and the American Museum of Natural History. A single specimen is reported by Schoener to reach 52.5 mm (AMNH 49845 from "25 mi N Aux Cayes, Jeremie Road" [corrected by Thomas and Schwartz to "32 miles from Aux Cayes on the Jeremie Road" from Hassler's field notes]). This locality is well within the range of *monticola monticola* and is one of the Hassler specimens reported by Williams (1962) as *A. monticola* and so regarded also by Thomas and Schwartz. It is this specimen that provided the 55 mm record (Schwartz, personal communication). It is now clear that this specimen is not *monticola* (see below).

In the relatively large series that the Museum of Comparative Zoology now possesses from the Castillon ravine and from other localities no male *monticola monticola* exceeds 45 mm in snout-vent length; this size is exceeded by female *rupinae* (46 mm snout-vent length) from Castillon. The Schwartz collection of *monticola monticola* has no male with a snout-vent length greater than 42 mm. *A. m. quadrisartus* is somewhat larger: Schwartz (personal communication) reports males of 48 mm snout-vent length. Thus no veritable specimens of *monticola* or *quadrisartus* are known to reach the 55 to 57 mm snout-vent length of Castillon *rupinae* or of AMNH 49845.

The latter specimen has been a source of confusion in more than size. It was cited by Williams (1962) as the basis of a description in life for male *monticola.* We quote again the description which is taken from W. G. Hassler's field notes:

"General dorsal color Hooker's Green. Saddles brown green, three in number, narrowest middorsally, one across shoulder, two between fore and hind legs. A light crescent in the temporal region. Throat and belly dark olive green. Legs barred. Tail barred. Eyes Antwerp Blue, sometimes changing to greenish. Edge of orbit yellowish brown. Skin of fan (which is relatively small) blue, scales light and dark green. Occurring also in a dark phase almost without pattern."

From the vantage point of present knowledge this description cannot be matched with either *rupinae* as known from Castillon or *monticola* or *quadrisartus.* Unmentioned are such diagnostic elements of color pattern as the flank stripe of *rupinae* and the two or the four ocelli of *m. monticola* and *m. quadrisartus.* The specimen itself as now preserved shows no pattern at all.

We may mention here two other difficult specimens (MCZ 124537–38). Both are males (43 mm and 49 mm in snout-vent length) collected by Webster at Catiche within the range of *quadrisartus.* Both are without *ocelli* and hence are clearly not *m. quadrisartus* or *m. monticola.* However, they were obtained in a lizard market, along with numbers of *m. quadrisartus,* and no detailed notes on color in life exist for them, nothing beyond the fact that one had a yellow belly and the other a red one.

We cannot on present evidence confidently refer either these two specimens or AMNH 49845 to *rupinae.* As preserved, one of the Catiche specimens shows the subcaudal white spots characteristic for *rupinae;* the other Catiche specimen does not, nor does AMNH 49845. Since the one Catiche specimen which had a red venter has also the white subcaudal spots in preservation, it may be truly *rupinae.* In the case of the other two, we call attention to the possible existence of still undescribed taxa and make no assignment of these specimens. We emphasize that our concept of *rupinae* rests solely upon the animals from the Castillon ravine.

It is worth noting that for neither *rupinae* nor the two subspecies of *monticola* is sexual dimorphism so marked as Schwartz assumed it to be for *monticola* when he included AMNH 49845

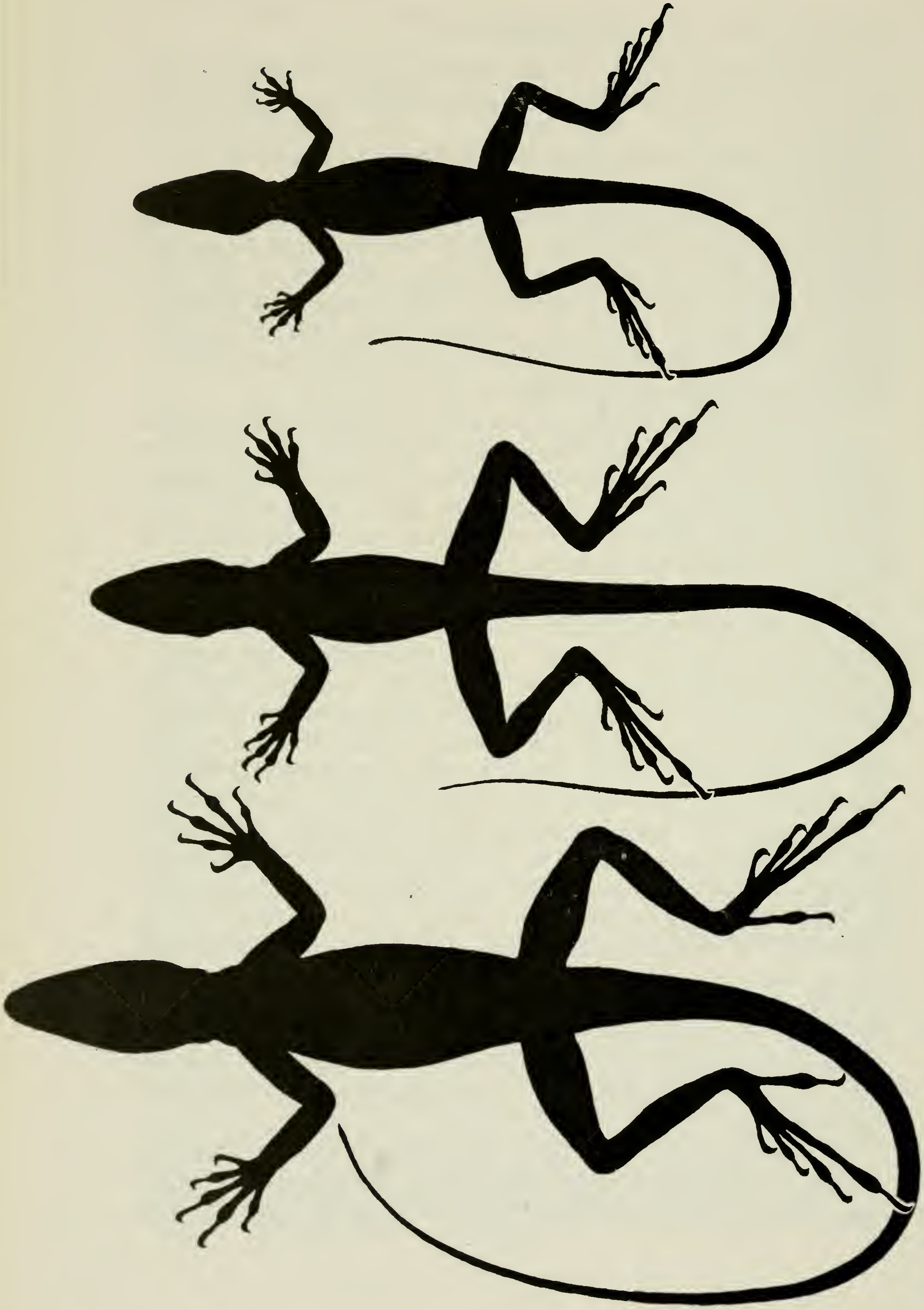


Figure 5. Body shape and size differences in species of the *monticola* group *sensu stricto*.

in that species. His ratio of maximum male size to maximum female size (55 mm to 39 mm) approximates 1.4. Our revised data show *monticola monticola* with maximum ♂ size 45 mm, maximum ♀ size 42 mm, equivalent to a ratio of 1.07. The comparable data for *m. quadrisartus* are ♂ 48 mm, ♀ 42 mm, ratio 1.14, and for *rupinae* ♂ 57 mm, ♀ 46 mm, ratio 1.24.

One other species of the *monticola* group appears very close to *rupinae.* In fact, the resemblances of *koopmani* to *rupinae* seem as close or closer than those to *m. monticola* or *m. quadrisartus* (Tables 1 and 2). Particularly striking is the red ventral coloration found in both *rupinae* and *koopmani,* but similar also is the presence of a flank stripe, the bluish dewlap, the throat spotting and the yellow or orange chin. The major color difference between *rupinae* and *koopmani* is the absence of transverse banding in *koopmani;* only in this aspect of color is *rupinae* closer to *m. monticola* and *m. quadrisartus.*

However, *A. koopmani* is a grass anole, and the adaptation has required a body shape different from that of *rupinae* or *monticola* (Fig. 5). In size also *A. koopmani* is distinctive; it is the smallest of this group of three related forms (♂ maximum size 42 mm, ♀ maximum size 35 mm, with a ratio therefore of 1.2).

A. koopmani has not before been explicitly referred to the *monticola* group. Rand (1961), however, in describing the species, did suggest that *A. monticola, darlingtoni* [now *etheridgei*], *christophei, hendersoni, baharucoensis,* and *Xiphocercus* [now *Anolis darlingtoni*] might, some or all of them, be closely related and that *koopmani*'s relationship might lie with these. We would certainly agree that *koopmani* has rather close affinities with all the species Rand named. However, from *rupinae*'s resemblances on the one hand to *monticola* and on the other to *koopmani,* it is now obvious that these three South Island species are a very tight group or subgroup of their own. That they are only a little less close to *A. rimarum* and related but more distantly to *A. etheridgei, A. christophei* and newly described *A. fowleri,* all North Island species (Tables 3 and 4), we will also affirm. We now, however, would distinguish between a *monticola* group *sensu lato* including both North and South Island species and a *monticola* group *sensu stricto* containing only the South Island species. The intimate relationship of the latter clearly separates them as a unit, as opposed to the significantly more diverse North Island set.

It is clear, therefore, that the description of *rupinae* (like Schwartz's recent discoveries of South Island *A. sheplani* and North Island *A. fowleri*) does nothing to diminish the intriguing differences between North and South Island montane faunas that were commented on by Williams and Rand (1969).

It is too early to do more than draw attention to a problem still unsolved. We are in no position to make dogmatic statements about the montane fauna or faunas. To cite only one example, the genus *Chamelinorops,* which on reasonable grounds was thought to be a South Island endemic or even autochthon (Thomas, 1966) is now known by a single juvenile from the middle of the Cordillera Central (MCZ 126708 from Limoncito, southwest of Constanza, La Vega Province, Dominican Republic) collected by T. P. Webster. In such cases of rare or local species, no safe judgments will be possible until montane Hispaniola is much better known than it is now. Nevertheless it is worth noting that at present no parallel is known in the North Island montane fauna to the South Island close-knit triplet of *monticola, rupinae* and *koopmani.* The North Island set of species are each very distinct from one another morphologically and in color and in ecology. The discontinuities are very sharp, so sharp that their association as a group is not beyond question. This is very different from the South Island series.

HABITAT, CONGENERS, ECOLOGY

The type locality.

Castillon is a market place and a diffuse village at a low point in one of several ridges extending north from the Massif de la Hotte. The surrounding country is dry and highly disturbed. Land not used for subsistence agriculture or pasture is covered by brush. Within this area *A. rupinae* occurs in the small pocket of damp and shady habitat in a ravine visible from the hill north of Castillon. About 200 meters south of the market stalls the road bends sharply, and at this point there is a well-worn trail along the side of the ridge. At first it traverses generally open slopes, but after a little more than one kilometer the trail enters the ravine near the base of a cliff. Between the cliff and the trail there is a fairly level area 12 to 15 meters long and 4 to 6 meters wide, where all specimens of *A. rupinae* were collected.

Only a few medium to large trees grow within the ravine. The rocky ravine floor and surrounding slopes are, however, covered by a thick growth of brush. Because of the cliff and the steep hillsides, the ravine floor is sheltered from the sun. On July 2, 1970 sunlight did not reach the cliff base until 9:30. Water trickles over and seeps from the base of the rock wall. Mosses and similar plants flourish on moist and shaded rocks. Below the trail the ravine is steep and filled with broken rock. It soon widens and becomes more exposed.

The anoline lizards of the Castillon area.

In September, 1969 and in June, 1970 the fauna of this area was sampled by organizing lizard markets in the Castillon market place and by collecting during the day and night around and within the ravine. Only *A. distichus* and *A. coelestinus* are abundant and generally distributed in the region. Both occur on the exposed slopes around the ravine but not within it. A third widespread and essentially lowland species, *A. cybotes,* is much less common. It does occur in some numbers on rocks along the trail entering the ravine and in the ravine itself. Two specimens of *A. ricordii* were procured from a lizard market.

Four species occurring here are considered montane, since they are unknown from coastal localities. (1) *A. hendersoni* is uncommon around Castillon, at least along the trail to the ravine. A single specimen was collected near the market place, and two were taken in trail-edge vegetation near the ravine. (2) On the ravine floor and along its approaches *A. monticola* is abundant. While this species occurs throughout the brush in the ravine up to the periphery of some bordering garden areas, it is absent from drier brush patches on the hillsides. (3) A single *Chamelinorops barbouri* was found along the trail near the ravine. (4) The total area inhabited by the population of *A. rupinae* is probably quite small. All specimens were collected from a very short segment of the ravine floor. Perhaps it also occurs on the surrounding cliff and slopes of broken rock. It seemed much less common in 1969 than in 1970.

Of these anoline species, *A. rupinae* seems to have the strongest requirement for cool, moist conditions. *Anolis monticola* is the only other species common on the ravine floor, but it also occurs on the sides of the ravine. *Anolis cybotes* occurs within the ravine close to *A. rupinae,* but the two species seem to have exclusive microdistributions. The other species seem to be intolerant of the ravine environment or were observed too infrequently for any statement on co-occurrence with *A. rupinae.*

A syntopic sibling?

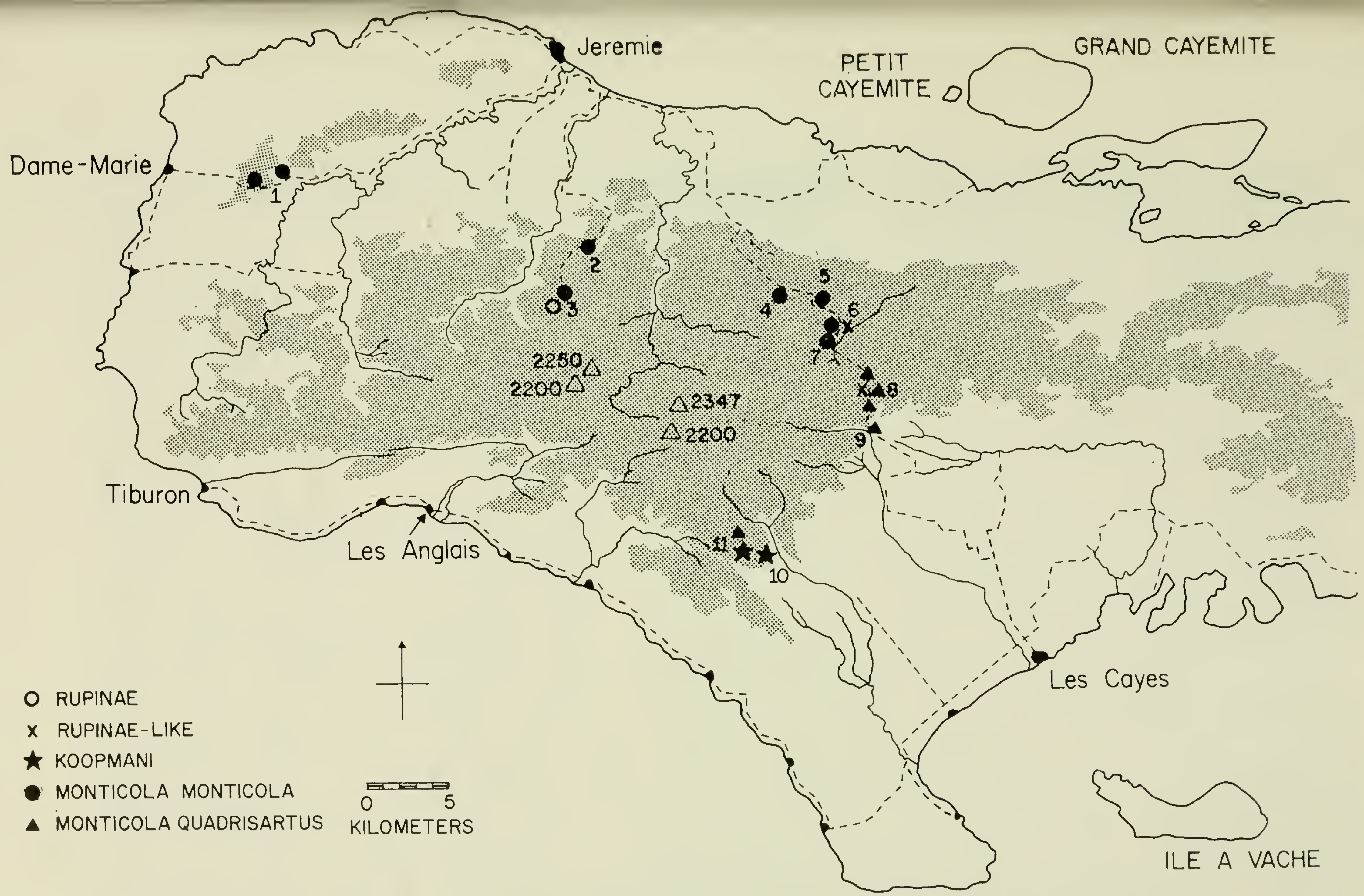
In one regard *A. rupinae* appears to be unique among anoles. This may be a defect of our present information, but *rupinae* is currently known only *within* the immediate habitat of *A. monticola.*

It is worth emphasizing that, if confirmed, this is a special situation. *A. rupinae* is close enough structurally to *A. monticola* to be called a sibling of the latter, that is some museum specimens and perhaps females in the field have been (see above) or could be confused. Many such sibling pairs are known in the West Indies, sometimes sibling only in the sense of closest relatives, sometimes in the more usual sense of both close relatives and barely distinguishable (under some, usually museum, conditions). However, such siblings ordinarily are either distinct in climatic preference and hence allotopic or they are para- or allopatric (as *A. rupinae* appears to be to *A. koopmani*).

Possibly *A. rupinae* does occur somewhere separately from *A. monticola.* Certainly *A. monticola* is known from a number of localities at which *A. rupinae* is not known. However, it can be pointed out already that the sharply different color patterns of these two species (and the dewlap difference at Castillon) and the striking difference in size are the kinds of adaptations — the color patterns for species recognition, the size difference for avoidance of competition for food — that syntopic or widely overlapping anoles have evolved in many instances (the Schoener rules, Schoener 1970, Williams 1972). That *rupinae* appears to be even more rigidly tied to shaded and moist situations than is *monticola* does not damage the suggestion that *rupinae* and *monticola* are consistently syntopic. On the contrary, this presumed greater shade and moisture preference of *rupinae* makes it all the more likely that its preferred habitat is *within* the habitat range of *monticola.* (From the evidence of Castillon *rupinae* does not exclude *monticola.*)

The *monticola* group *sensu stricto* — an unusual miniradiation

The status of *A. rupinae* and *A. monticola* as unusual siblings is compounded by the close relationship of both to *A. koopmani.* While certainly not a sibling — divergence in scale counts, habitus and size are all reasons for its previously uncertain affinities — the presence of this third species in the same small mountain mass is evidence that the *monticola* group *sensu stricto* has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GRAND CAYEMITE
Dame-Marie
Tiburon
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O RUPINAE
x RUPINAE-LIKE
★ KOOPMANI
● MONTICOLA MONTICOLA
▲ MONTICOLA QUADRISARTUS
0 5
KILOMETERS

Figure 6. Distribution of *monticola* group *sensu stricto,* including the unassigned specimens. Localities: 1: 7.5 and 10 km (airline) WSW Moron; 2: 5 km (airline) SSE Marché Léon; 3: Castillon, 1.3 km SSW Castillon; 4: 1.5 km S Beaumont; 5: Carrefour Zaboca; 6: Trou Bois (1.3 km NNE Duchity); 7: 1 km S Duchity; 8: Catiche area, from the high point in the road to the southern edge of the plateau, including Tombeau Cheval; 9: side of Ravine du Sud near Post Advance; 10: Carrefour Canon, near Ducis; 11: Les Platons. Shaded area exceeds 400 m elevation.

evolved differently from most other anole species groups. All three are known from moderate elevations (1000′ to 3000′) (Fig. 6), although the lower bound is far more meaningful than the upper one. Even with the inclusion of *A. koopmani,* climatic divergence in the *monticola* group seems relatively limited.

Unfortunately, distributional and ecological information is so scant that interactions among these species are an open problem. Only *A. monticola* has an extensive distribution. A series of samples taken along the Les Cayes to Jeremie road indicates that the subspecies *monticola* and *quadrisartus* are separated by the Rivière Glace, a stream originating south of Duchity and flowing north, disappearing into limestone hills. While *A. rupinae* as described is known only from Castillon, the unassigned specimens from two collections on the Les Cayes to Jeremie road suggest the possibility of a broader distribution and contact with both subspecies of *monticola.*

The scarcity of records for *A. rupinae* is understandable, since its deep shade habitat is limited and very patchy in the highly disturbed mid-elevations of the Massif de la Hotte. The apparent restriction of *A. koopmani* to the Les Platons region is more enigmatic. It can be common in a shaded coffee patch or in the open brush growing in an abandoned citadel. Even on the Les Platons plateau it does not always occur in such vegetation and it appears to be absent also in comparable areas along the Les Cayes to Jeremie road. T. C. Moermond has studied the anoles of the Les Platons area and discovered *A. monticola,* but as yet it has not been collected syntopically with *A. koopmani.* (Recall that as *A. rupinae* is larger than *A. monticola, A. koopmani* is smaller (Fig. 5)). Moermond (MS) has documented structural habitat and foraging differences for the two.

The unusual karyology of the *monticola* group *sensu stricto* has special interest in the context of the morphological, geographic and ecological relationships of its members. Departures from the ancestral anoline condition that occur in the complements of all three can be attributed to centric fission (Webster, *et al.,* 1972), a process that is known in few alpha anoles. Of the six ancestral pairs of metacentric macrochromosomes, five or six have fissioned in *A. monticola* to yield diploid numbers of 46 to 48. Two pairs fissioned to produce the diploid number of 40 in *A. koopmani.* As in *A. monticola,* in *A. rupinae* there is polymorphism for macrochromosomal number with an inferred range from six to eight pairs (i.e. none to two pairs fissioned).

In addition, *A. rupinae* seems to have one more pair (thirteen) of microchromosomes than the ancestral complement (twelve), a condition not previously reported. Whether this additional pair originated by microchromosomal fission or in the course of change in macrochromosomal number and morphology is unknown.

In addition to supporting the obvious close relationships within the *monticola* group *sensu stricto,* the shared class of chromosome change — fission — may have been critical in the origin and divergence of these species. A role for karyotypic differentiation in the partial or complete genetic isolation of two populations has been suggested by several authors (see Mayr, 1970; White, 1973; Hall, MS). In addition, chromosomal changes are key elements in more complex evolutionary scenarios which envision "cascading revolutionary speciation" (Hall, MS) or a genetic release that accompanies extensive fissioning and favors adaptive radiation (Todd, 1970). The components of these more elaborate hypotheses — genetic revolutions, genetic effects of fission, chance karyotypic change in small populations — are at present individually such poorly documented phenomena that the larger constructs are particularly open to criticism (see White, 1973 on Todd, 1970). We suggest that the derived and complex karyology of this small assemblage of anoles merits further study, both as a possible aid to understanding their miniradiation but more importantly as a system that may be relevant to larger evolutionary issues.

ACKNOWLEDGMENTS

The discovery and study of *Anolis rupinae* have been supported by NSF grants B 019801X and GB 37731X to E. E. Williams. We owe warm thanks to Lamy Camille of Port-au-Prince for help with field work and to A. Ross Kiester for companionship and assistance during the trip which first obtained *rupinae*.

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Table 1

Scale counts — the South Island species: the *monticola* group *s. str.*

	rupinae	*monticola*	*koopmani*
scales across snout at level of second canthal	9–15	7–11	7–9
scales between supraorbital semicircles	1–3	2–4	1–3
interparietal/ear	≤	≤	<
scales between interparietal and supraorbital semicircles	3–6	3–6	3–5
loreal rows	6–9	6–9	5–8
scale rows between subocular and supralabials	0–1	0–1	0
supralabials to center of eye	5–6	6	5–6
middorsal rows enlarged scales	2–3 (raised into a ridge)	2–3 (raised into a ridge)	6–9 (not raised into a ridge)
ventrals	keeled	keeled	keeled
lamellae under phalanges ii and iii of fourth toe	16–22	14–19	17–19
dewlap	+ small ♂, absent ♀	+ small ♂, absent ♀	+ small ♂, absent ♀

Table 2

Color — The South Island species: the *monticola* group *sensu stricto*

	rupinae	*monticola monticola*	*monticola quadrisartus*	*koopmani*
color of venter	red orange, rarely yellowish	yellowish green		yellow tinged with red
dewlap color	sky blue	yellow to reddish orange	blue to bright yellowish green	blue skin + yellow scales
chin color	yellow	blue to blue green	bluish	orange pink
ocelli	—	2 nuchal ocelli — black with blue centers	2 nuchal + 2 on nape — black with blue centers	—
flank stripe	+	—	—	+
spotting on throat	+	—	—	+
transverse banding	+	+	+	—
middorsal stripe	in female	in female	in female	in female

Table 3

The North Island species of the *monticola* group: scale counts

	rimarum	*etheridgei*	*christophei*	*fowleri*
scales across snout at level of second canthal	7–10	8–15	6–10	5–7
scales between supra-orbital semicircles	0–1	0–4	1–2	0–1
interparietal/ear	= large ear	<	<	> small ear
scales between inter-parietal and semicircles	2–3	3–6	3–7	1–2
loreal rows	4–6	5–10	4–8	5–6
scale rows between subocular and supralabials	0	1	1	0
middorsal rows enlarged	2	0	0	0
ventrals	smooth	smooth	smooth	smooth
lamellae under phalanges ii and iii of fourth toe	16–23	15–21	18–25	17–21
maximum size ♂	45 mm	43 mm	49 mm	77 mm
dewlap	small	small	large	large (in both sexes)

Table 4

The North Island species of the *monticola* group: color

	rimarum	*etheridgei*	*christophei*	*fowleri*
color of venter	pale yellow-green	tannish	yellow to greenish yellow	brown or green
dewlap color	white scales and dull greenish orange skin	white or white with gray base	pale purple	brown or brown with yellow periphery
chin color	whitish	pale green ♂ or cream with brown striae	dark gray	brown or green
ocelli	none	none	none	none
flank stripe	present	none	present	in females and juveniles
spotting on throat	none	none	none	none
transverse banding	grey to black butterfly marks wide transverse or bands	usually bands in ♂, not in female	bronzy or greenish brown blotches	brown bands in females
middorsal stripe	a light stripe more conspicuous in females	often a bronzy zone in ♀	none	in females and juveniles, joined to flank stripe by diagonal bars

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ANOLIS MARCANOI NEW SPECIES: SIBLING TO *ANOLIS CYBOTES*: DESCRIPTION AND FIELD EVIDENCE

ERNEST E. WILLIAMS[1]

ABSTRACT. A new species, *Anolis marcanoi,* very close to *A. cybotes,* is described from the southern slopes of the Cordillera Central in the Dominican Republic. Differing from *A. cybotes* primarily in the species recognition character of a red rather than a white or grey dewlap, it appears to be surrounded by populations of *A. cybotes* and is also sympatric with that species in a considerable part of its known range. Ecological differences between the two species are not obvious, and it is possible that neither is able to displace a resident population of the other.

In December 1966, Joel D. Weintraub, collecting in the Dominican Republic, brought back from San Jose de Ocoa two small lizards which in general morphology and in scale characters appeared to be assignable to the species *Anolis cybotes.* These specimens, although clearly juvenile, had rudimentary reddish dewlaps. The color of the dewlaps immediately attracted attention, since all the then known populations of *A. cybotes,* a species widely distributed throughout Haiti and the Dominican Republic, had yellow or grayish, more rarely orangish pigmentation in the dewlap but never red except in populations at the extreme end of the Southwest Peninsula of Haiti, which, while having a reddish dewlap, have also more or less keeling on chest and belly scales, while the red-dewlapped form from San Jose de Ocoa had perfectly smooth chest and belly scales.

A search for the population from which Weintraub took his specimens began in 1968, and over several subsequent summers the evidence has built up that the red-dewlapped *cybotes*-like

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[1] Museum of Comparative Zoology, Cambridge, Mass. 02138

Anolis is a new species quite distinct from *A. cybotes* in electrophoretic characters but nearly indistinguishable in squamation and identical in karyology[1]. The two species overlap spatially in a complex way.

The new species is named for Professor Eugenio de Jesus Marcano F., who helped so much in early investigations in the Dominican Republic.

Type. MCZ 131837, an adult male from ca 5 km N La Horma, Peravia Province, Dominican Republic, collected by Jonathan Roughgarden and local inhabitants, 18 July 1972.

Paratypes. All from Peravia Province, Dominican Republic. Same locality as type: MCZ 131846–75, J. Roughgarden and local inhabitants collectors, 18 July 1972; MCZ 143437–43, P. E. Hertz and R. B. Huey collectors, 2 August 1974. Lizard markets vicinity of La Horma: MCZ 131824–42, local inhabitants collectors, 19 July 1972; 1 km N Malaqueta on road to Valle Nuevo, W. E. Hall, E. J. Marcano and E. E. Williams collectors, 1 July 1969; below pines, Sabana Larga, N of San Jose de Ocoa: MCZ 117810, W. E. Hall, E. J. Marcano and E. E. Williams collectors, 1 July 1969; San Jose de Ocoa: MCZ 104402–03, J. Weintraub collector, 21 December 1966; 1.3 mi S San Jose de Ocoa, 1400 feet: V 34068–79, A. Schwartz and local inhabitants collectors, 19 November 1971; bridge over the Rio Ocoa S San Jose de Ocoa: MCZ 107072–76, A. S. Rand, E. J. Marcano and E. E. Williams collectors, 27 July 1968; MCZ 117809, 118606, W. E. Hall, E. J. Marcano and E. E. Williams collectors, 1 July 1969; MCZ 143247, P. E. Hertz and R. B. Huey collectors, 22 July 1974: 3–5 km S San Jose de Ocoa: V 21392–95, R. K. Bobilin and R. Thomas collectors, 24 July 1969; 16 km N Cruce de Ocoa: MCZ 143246, P.E. Hertz and R. B. Huey collectors, 21 July 1974; 12 km N Cruce de Ocoa: MCZ 143245, P. E. Hertz and R. B. Huey collectors, 22 July 1974; 3 km N Cruce de Ocoa, 500 feet: V 35815, A. Schwartz and local inhabitants collectors, 27 December 1972; coconut grove near Las Carreras on road to San Jose de Ocoa, MCZ 115640, W. E. Hall, E. J. Marcano and E. E. Williams collectors, 1 July 1969; Las Mayitas, 27 km S San Jose de Ocoa,

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[1] Like *A. cybotes* the new species has the 12 macrochromosome, 24 microchromosome karyotype that occurs so frequently in iguanids and other lizards (W. Hall, personal communication).

550 feet: V 15645, V 15598, J. K. Lewis collector, 3, 5 August 1968; 6 km N of Bani on road to El Recodo (just S of the first ford), P. E. Hertz and R. B. Huey collectors, 20 July 1974; La Jina, 7–8 km N of Bani on road to El Recodo: MCZ 143241–43, 143248–49, 143262, natives for P. E. Hertz and R. B. Huey collectors, 20 July 1974; MCZ 143244, P. E. Hertz and R. B. Huey collectors, 2 August 1974; 11 km N of Bani on road to El Recodo: MCZ 143253–55, P. E. Hertz and R. B. Huey collectors, 20 July 1974; 12 km N of Bani on road to El Recodo: MCZ 143256–61, P. E. Hertz and R. B. Huey collectors, 20 July 1974; 13 km N of Bani on road to El Recodo: MCZ 143250, P. E. Hertz and R. B. Huey collectors, 20 July 1974.

Head. Head moderately massive, snout to posterior border of eye about as long as tibia. Head scales mostly smooth. Five to nine scales across snout between second canthals. A shallow frontal depression. Naris in front of canthal ridge. Anterior nasal scale (sometimes divided) in contact with rostral.

Supraorbital semicircles in contact or separated by one scale row, separated from the supraocular disks by single rows of granules. Supraocular disks consisting of about six to eighteen enlarged weakly keeled scales separated by about five rows of scales and granules from the scales of the supraciliary rows. One or two elongate supraciliaries continued posteriorly by a double row of moderately enlarged scales. Canthus distinct, canthal scales four, the second largest. Loreal rows four to seven, the lower rows larger. Supratemporal area granular, grading into moderately enlarged scales surrounding the interparietal. Interparietal slightly larger or slightly smaller than ear, separated from the supraorbital semicircles by one to three scales.

Suboculars separated from supralabials by one row of scales or in contact, anteriorly grading into loreals, posteriorly grading into large scales at the corner of the mouth. Six supralabials to the center of the eye.

Mentals broad as long, usually in contact posteriorly with four small throat scales. Infralabials narrow, in contact with two to three large sublunate sublabials. Throat scales small, swollen, not keeled; only the anterior ones elongate.

Trunk: Middorsal scales not *abruptly* larger than flank scales (Fig. 1, compare also figures in Williams, 1963). Ventrals much larger than middorsals, cycloid, smooth. Postanal scales enlarged, often broken into four.

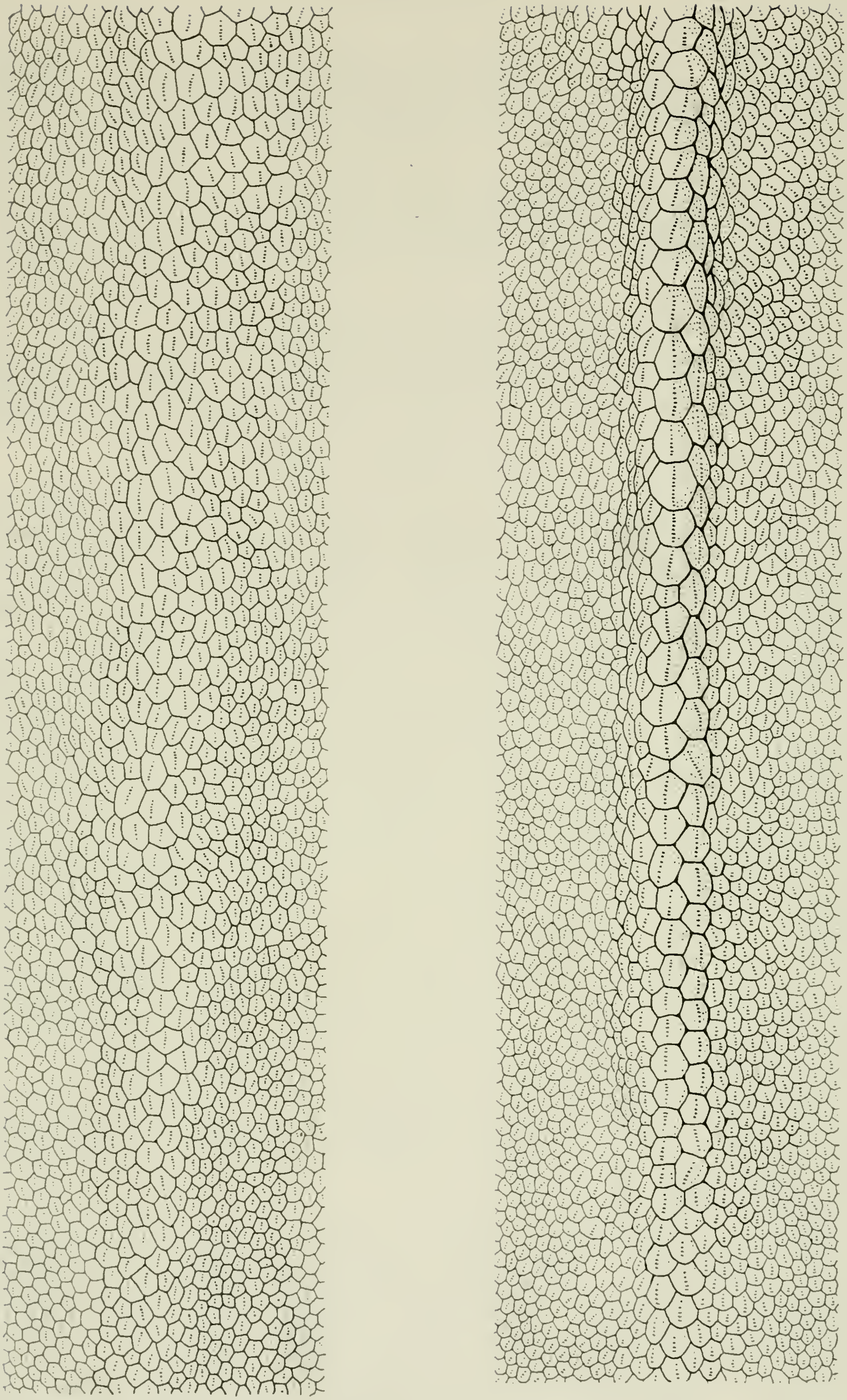


Figure 1. Dorsal scales. Left: *Anolis marcanoi,* Paratype, MCZ 107075. Right: *A. cybotes,* MCZ 115641. Both from the bridge over the Rio Ocoa south of San Jose de Ocoa, Peravia Province, Dominican Republic.

Gular fan. Large, scales smooth, no larger than ventrals.

Limbs and digits. Hand and foot scales multicarinate. About 15–22 scales under phalanges 2 and 3 of fourth toe. Largest scales of arm unicarinate, of leg smooth or very weakly multicarinate; those of arm smaller, those of thigh larger than ventrals.

Tail. Compressed, each verticil surmounted by four sharply keeled scales, ventrally three pairs of somewhat larger, strongly keeled scales.

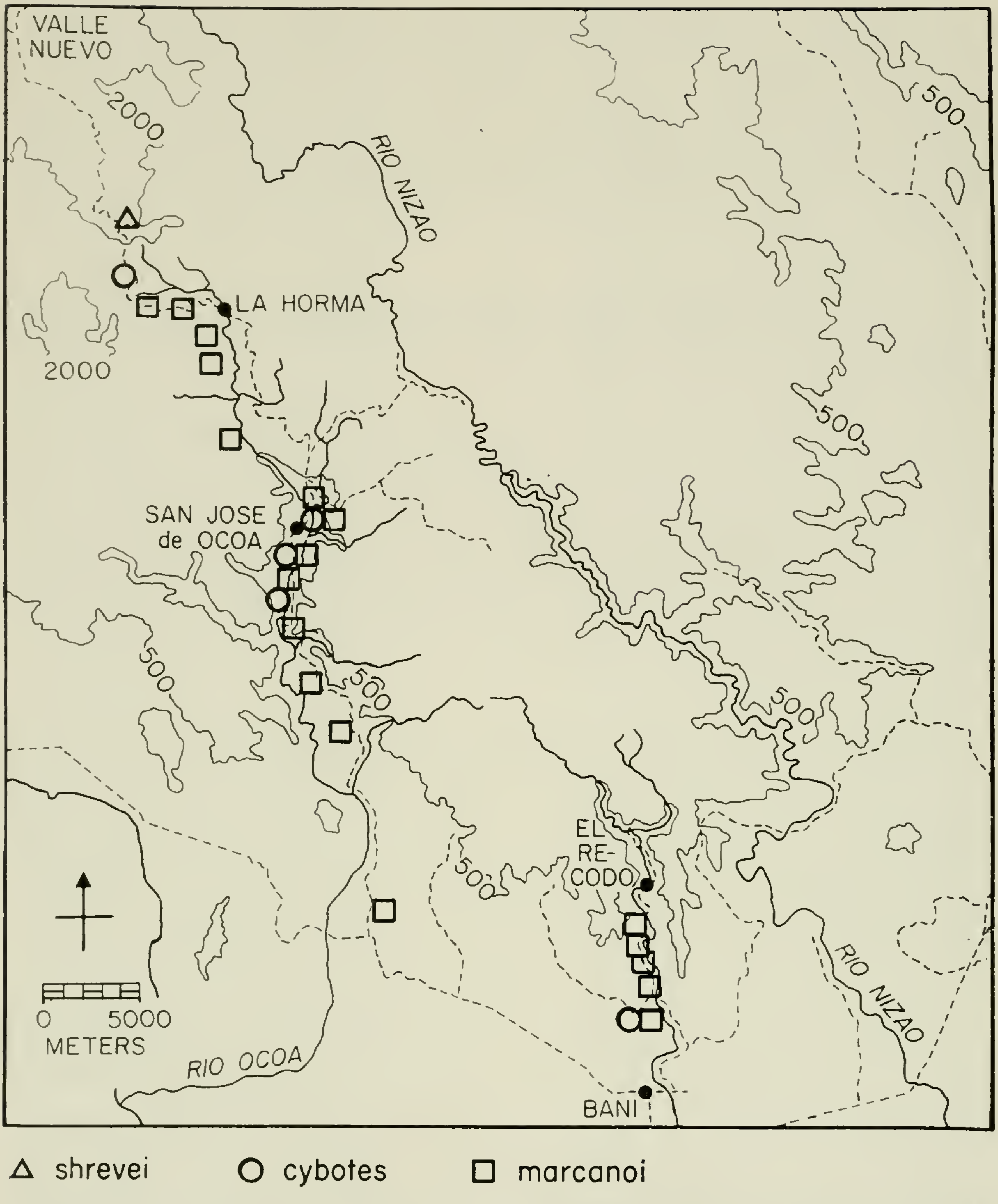
Color. Brown with or without obscure dorsal blotching, head sometimes distinctly reddish. Dewlap in males distinctly rose-red at the edge, more orangish anteriorly and posteriorly, but purplish or even bluish toward the center, the colors grading into one another. Females with vestigial red-ringed throat fans and *usually* distinct longitudinal dark streaks on the white of chin and throat.

Differential characters. On the classic characters conventionally used in *Anolis,* especially *preserved Anolis, A. marcanoi* is a poorly differentiated species. No scale characters will consistently separate *marcanoi* from *cybotes.* (From the geographically adjacent related montane species, *A. shrevei* as well as *A. whitemani* of the arid lowlands to the west, *A. marcanoi* is amply distinct by its smooth rather than keeled ventrals.)

Some specimens of *marcanoi* have almost no enlargement of the middorsal scales anywhere on the dorsum: in most the sacral area shows the middorsal scales minimally or not enlarged. However, some specimens of *cybotes* and *marcanoi* — both sexes and all ages — are impossible to distinguish by this character, i.e. in these animals of both species the middorsal scales are weakly enlarged. No other scale characters seen are even as useful as this.

Color, then, is the major differential character, the male dewlap being especially obvious, but the red in the throat of females is also highly diagnostic.

Distribution. The distribution of *A. marcanoi* is curiously complex (Fig. 2). It is recorded from the area just south of the first ford on the road to El Recodo, north of Bani (here *A. cybotes* is also present), and from La Jina, the village just beyond the first ford (no *cybotes* obtained). *Marcanoi* is known as far


VALLE NUEVO
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EL RE-CODO
RIO NIZAO
0 5000 METERS
RIO OCOA
BANI
△ shrevei
○ cybotes
□ marcanoi

Figure 2. The known distribution of *Anolis marcanoi.* Squares: *A. marcanoi.* Circles: *A. cybotes.* Triangle: *A. shrevei.*

north on this road as the second ford, and presumably beyond it, but this ford is impassable in a rental car. The new species occurs also on the slopes of Loma de Pinos, just east of the road which connects Constanza in the Cordillera Central via San Jose de Ocoa with the road west from Santo Domingo to Barahona. There are only sight records from this area. North of Cruce de Ocoa on the west road there are occasional records of *marcanoi* south of San Jose de Ocoa; in these instances it is found on fence posts or in coconut groves, apparently as enclaves with a wider but sparse distribution of *cybotes* in the surrounding acacia. At the bridge just south of San Jose de Ocoa, and inside or in the immediate environs of the city, both species occur broadly intermingled. North of the city as far as La Horma, *A. cybotes* is known only from lizard markets in villages, while *A. marcanoi* was collected on rocky hillsides, i.e. *cybotes* now appears as enclaves within populations of *marcanoi.* At lizard markets up to 4 km N of La Horma only *marcanoi* was obtained. A single specimen of *marcanoi* is known from 9 km N of La Horma. At 13 km N of La Horma *cybotes* reappears and, on the evidence of three specimens of this species and no examples of *marcanoi,* appears to separate *marcanoi* from *Anolis shrevei,* another *cybotes* relative living on the peculiar cold plateau of Valle Nuevo.

Many more specimens have been seen and even collected than have been preserved. Some of the material used for electrophoresis was collected by Thomas Jenssen from nine localities within or near the city of San Jose de Ocoa: 8 km N San Jose de Ocoa on road to Nizao, 2 km north of the city under the bridge over the Rio Ocoa, 8 km N on road to La Horma, at the school in the southwest end of town, 3 km W on road to El Pinar, 2 km S at bridge over the Rio Ocoa (and along the river itself), 3 km S along a small tributary of the Rio Ocoa.

In the vicinity of San Jose de Ocoa the two species occur *almost* syntopically but nevertheless with some tendency to exclusion. It is not easy anywhere to define an ecological difference between the two species. The association with rocky, very open hillsides is definite for *marcanoi* in the vicinity of La Horma (hence at relatively high elevations), but in the lowlands near the intersection with the west road *marcanoi* is known from a shaded coconut grove. Presumably some combinations of temperature and humidity may provide different optima for the two species, but this is a physiological question not yet worked out.

DISCUSSION

"Sibling species."

It becomes more and more obvious that, in addition to those species in which museum taxonomists rejoice because they are very distinct in terms of the characters conventionally studied, there are in many groups valid biological species only imperfectly separable on museum characters, if at all. This phenomenon is only interesting in terms of the history of museums, not of biology. Museum techniques alter as taxonomy progresses. It will not be necessary in the near future to defend or specially comment on cases like that here described. Given that species status should be recognized by any taxonomist on the full suite of characters known for any population and not on the basis of some subset selected because of convention or convenience, it is inevitable that *marcanoi* be recognized as a full species.

The two juvenile specimens on which the discovery of *marcanoi* was based lack any trace of gular red after eight years in alcohol. It would be difficult or impossible to separate them as a distinct taxon now, were they all that was available. But this is a failure of techniques, a museum failure like the failure of a library with books printed with impermanent ink.

The biological phenomenon in *marcanoi* and *cybotes* that is interesting is the way in which they overlap. On a large scale map, *marcanoi* and *mybotes* do overlap over a considerable distance. Macro-geographically they are in part sympatric, but quite clearly they are rarely syntopic. *A. cybotes* and *A. marcanoi* are in this regard rather similar to the Cuban *homolechis-allogus-sagrei* series. As with *marcanoi* and *cybotes,* these color differences and dewlap differences are more reliable than scale differences; the latter are in fact few, minor, and usually bridged by intrapopulational variation. In the Cuban series, as with *marcanoi* and *cybotes,* there may be close physical juxtaposition. A walk down a path through the woods on a Cuban finca might find two species on adjacent trees, three species not far from one another, but close examination would show that one species lived in deep shade, one in half shade, one in open sun. Where the environment, at the edges of these different habitats, juxtaposed the three conditions of shade, half shade and sun, the lizard species would also be juxtaposed, while where the environment was homogenous over a larger area, there the lizard populations would also be homogenous (Ruibal, 1961; Ruibal and Williams, 1961).

The relations between *marcanoi* and *cybotes,* however, appears to be subtler than that in the Cuban series. An inadvertent experiment may demonstrate this point. The first series of *marcanoi* were taken in a grove of trees on the right bank of the river at the bridge over the Rio Ocoa south of San Jose de Ocoa. Only *marcanoi* was taken in this situation. In several subsequent summers the grove of trees has been occupied by *cybotes,* never by *marcanoi,* which instead has been found on rocks and fenceposts on the open road above the grove. Our latest observations found the area considerably altered and on the day of observation neither species was taken in the grove. Our first ecological judgment based on collections in the grove during the first year were that *marcanoi* preferred shade and *cybotes* (presumably) sun. But subsequent multiple observations both at the grove by the river and elsewhere have demonstrated this conclusion to be wrong. Apparently *cybotes* and *marcanoi* do not respond to the environment as litmus paper does to acid or base, or as the Cuban species more nearly seem to do. On the contrary, simple physical possession seems to be part of the story. By the act of collecting we cleared an area of *marcanoi. Cybotes* was the species that moved in and has held this small area ever since. There may thus be situations — perhaps many situations — in which the advantage to either species is so marginal that it cannot dispossess a population in residence.

By this hypothesis *cybotes* and *marcanoi* differ as little physiologically as they do morphologically. If this be true, it is especially interesting that the electrophoretic evidence presented by T. P. Webster in *Breviora* 431 shows that the genetic base for these very similar morphological and physiological phenotypes is so sharply different. It is once again a lesson that phenotypic similarity is an imperfect clue to the continuity of genetic systems. Clearly no evidence can be neglected if our object is to establish the reality of genetic discontinuity.

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AN ELECTROPHORETIC COMPARISON OF THE HISPANIOLAN LIZARDS *ANOLIS CYBOTES* AND *A. MARCANOI*

T. Preston Webster[1]

Abstract. Samples representing four localities — one for both species, two for *A. marcanoi,* and one for *A. cybotes* — were examined. Results for 24 polypeptides are reported, of which 21 were studied in all individuals. With each of 10 proteins individual identification is unequivocal or nearly so. These data confirm the presence of two species in Peravia Province of the Dominican Republic, verify the recognition of the red-dewlapped form as the new species *A. marcanoi,* and indicate that successful hybridization and introgression must be rare, if they occur at all.

Anolis cybotes and the newly described *A. marcanoi* (Williams, 1974) are so similar in morphology that no scale character will consistently separate them. The latter was recognized only because its red dewlap contrasts with the yellow one of the former. For anoles such a difference in dewlap color probably is important for reproductive isolation (Rand and Williams, 1970; Webster and Burns, 1973). In addition, populations of the two have been found side by side, but individuals are not known to mingle freely. This interaction, which is characteristic of closely related anoles, and the difference in dewlap color together provide sufficient evidence for the description of *A. marcanoi.* However, the great similarity of the two species invites additional information on the extent to which they have diverged and perfected reproductive isolation. I report here a study that used starch gel electrophoresis to examine some of their enzymes and nonenzymatic proteins.

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MATERIALS AND METHODS

Seven samples were examined. Of 62 individuals collected in October 1970 by T. A. Jenssen in the vicinity of San José de Ocoa, Peravia Province, Dominican Republic, 42 were red-dewlapped *A. marcanoi* (sample 3a) and 20 were yellow-dewlapped *A. cybotes* (sample 4a). In July 1974 E. E. Williams, R. B. Huey, P. E. Hertz, and R. Holt collected the remaining Peravia Province samples: additional short series of both species from San José de Ocoa (samples 3b and 4b) and *A. marcanoi* from La Gina (sample 1) and from the type locality, 5 km N of La Horma (sample 2). Sample 5 consists of 4 individuals from Debarasse, Departement du Sud, Haiti, a locality a few kilometers to the west of Jérémie, the type locality for *A. cybotes.* The Jenssen collection was shipped alive to Cambridge where the lizards were bled and frozen, but all other series were frozen in the field.

Methods of sample preparation and horizontal starch gel electrophoresis are derived from Selander *et al.* (1971). Protein stains and specific assays are similar to those current in work with vertebrates. Procedural details such as buffer systems best suited for each protein and minor modifications to published assay formulas are available from the author. With the exception of hemoglobin and a plasma protein, all proteins were examined in tissue homogenates. For some proteins, particularly indophenol oxidase, better results were obtained from lizards frozen in Cambridge than from those frozen in Hispaniola.

In many reports on genetic differentiation between vertebrate populations, including an earlier report on *Anolis* species (Webster, Selander, and Yang, 1972), the results are expressed as values of Rogers' coefficient of genetic similarity, S (Rogers, 1972). Unfortunately, in some circumstances the effect of this formula is counterintuitive. When a single locus is considered and no alleles are shared by two populations, the expected similarity is 0. If both populations are polymorphic, however, S is nonzero. The results of this study are presented as Nei's normalized identity of genes, I (Nei, 1972), which is consistently somewhat (2–7%) larger than S calculated for the same data.

For the computation of I, each polypeptide is treated as the product of a single gene.

RESULTS AND DISCUSSION

Among the polypeptides examined in whole animal homogenates, the bands representing 21 could be interpreted with sufficient consistency to be used in estimating relationships. Of these, eight indicate complete or almost complete differentiation of all populations of *A. marcanoi* from those of *A. cybotes* (Table 1). In addition, samples 3a and 4a apparently do not share variants of hemoglobin, plasma protein-1, and indophenol oxidase. For four of these proteins (hemoglobin, plasma protein-1, protein A, and lactate dehydrogenase-1) the difference in electrophoretic mobility is consistent, but so small that an individual expressing both variants could be confused with one producing a single variant. The differences for 6-phosphogluconate dehydrogenase, isocitrate dehydrogenase-1, phosphoglucomutase-1, alcohol dehydrogenase, albumin, and peptidase can be scored unequivocally.

Samples 3b and 4b and the majority of individuals in samples 3a and 4a were collected 2 km S of San José de Ocoa, along the bed and banks of the Rio Ocoa. At this locality the two species are common and in close contact. In such situations of parapatry or sympatry, discrete variation in the electrophoretic mobility of proteins can be more informative than morphological differentiation. Without genetic analysis or biochemical study of protein structure, interpretation of observed differences as allelic variation is generally correct (see Johnson, 1973, for criticism and enumeration of exceptions). Indeed, the inheritance of interspecific differences in some proteins has been observed in natural *Anolis* hybrids (Gorman *et al.,* 1971; Webster, unpublished); and patterns of phenotypic variation in anole populations can be explained by simple molecular and Mendelian models. Differences in phenotypic frequencies thus indicate the presence of reproductive isolation. Detection of isolation does not depend on absolute separation and could be inferred even from significant differences in allelic frequencies at a few loci. For these samples, each of 11 loci indicates an absence of allelic exchange. Species status for the populations has no reasonable alternative.

Since codominance is the rule for allelic variation at loci encoding proteins (it was observed for all of the protein variation within these samples), electrophoretic data can also be used to determine whether reproductive isolation is complete and whether occasional mismating leads to introgression. Thus the absence from the San José de Ocoa samples of a single individual heterozygous for one or more of the six clear allelic differences suggests that introgression between the two species must be rare, if it occurs at all. The samples are large enough to show that F_1 hybrid individuals must be uncommon but not so large as to exclude their occurrence. Of course, failure to detect hybrid individuals does not eliminate the possibility of attempted hybridization, whatever its frequency, if the issue of such unions is inviable.

A single individual in sample 1 of *A. marcanoi* is the exception to complete divergence of the two species on the basis of 6-phosphogluconate dehydrogenase variants. A heterozygote for the common variant of both species, it is not an F_1 hybrid (no *A. cybotes* were collected at this locality). This situation cannot be explained, nor does it require explanation. In extensive comparisons of sibling species the characteristic protein variants of one are often found in low frequency in the other (e.g., Prakash, 1969; Ayala and Powell, 1972; Webster and Burns, 1973). Had larger samples and more populations been considered, there probably would be fewer loci indicating absolute separation.

Conspecific populations are quite similar, both throughout the small known distribution of *A. marcanoi* and between *A. cybotes* samples separated by 420 kilometers. The unsatisfactory indophenol oxidase results — some individuals in sample 1 have a variant like that of *A. cybotes* — provide the only evidence for significant differentiation within *A. marcanoi*. Samples 4a and 4b of *A. cybotes* are essentially identical and are similar to sample 5 for all but one polypeptide (Table 1). If sample 5 is accepted as representing *A. cybotes* from the region of the type locality, then, of the two species around San José de Ocoa, that with the red dewlap has been correctly treated as the new species. The difference between intraspecific and interspecific levels of similarity is expressed as values of Nei's I in Table 2.

In nearly all interspecific comparisons involving at least 15 proteins, one or more has allowed an individual to be identified with complete or almost complete confidence. For instance, diagnostic proteins giving species assignment with 99% or greater certainty were found in each of several extensive comparisons of *Drosophila* sibling species (Ayala and Powell, 1972). In this comparison of *A. marcanoi* and *A. cybotes,* 10 proteins are diagnostic by the same criterion. Joint consideration of several, particularly the six having very distinct variants, should be sufficient to assign any individual to either *A. cybotes* or *A. marcanoi.* In fact, while the 1970 sample from San José de Ocoa was divided without error on the basis of dewlap color, for the 1974 sample it was necessary to use the electrophoretic results to correct some of the casual field identifications of juveniles and females. Three *A. cybotes* were misclassed as *A. marcanoi* and one *A. marcanoi* as *A. cybotes.*

Although unnecessary in the analysis of *A. marcanoi* and *A. cybotes,* the magnitude of a genetic similarity coefficient like Nei's I can be used arbitrarily to determine whether two allopatric populations merit species status. The proteins merely provide another class of phenotypic information to be used according to established taxonomic procedure, but the genetic interpretation is usually retained. A criterion for species recognition can be established in the context of several studies of populations at diverse taxonomic levels, as judged by morphology or observed reproductive compatibility. Similarity values for conspecific populations generally exceed 0.9, and exceptions are often associated with insular isolates or other distinctive evolutionary situations (see Selander and Johnson, 1973, for a review of such data). Infraspecific taxa showing some reproductive isolation differ at 10 to 25% of their loci, which is 10 to 15 times as much divergence as between local populations within those taxa (Ayala *et al.,* 1974). I feel that a similarity value of 0.7 or less indicates so much genic divergence that it is a fairly conservative criterion for species status. On this basis *Anolis marcanoi* certainly qualifies for recognition as a separate species: in comparisons with *A. cybotes,* $\bar{I}$ is 0.62.

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Table 1. Polypeptide Variation Within and Between Populations of *Anolis marcanoi* and *A. cybotes*.[1]

		Sample						
		1	2	3a	3b	4a	4b	5
Polypeptide, Variants[2]	N:	9	26	42	10	20	13	4
Albumin	a					1.00	1.00	1.00
	b	1.00	1.00	1.00	1.00			
Protein A	a	1.00	1.00	1.00	1.00			
	b					1.00	1.00	1.00
Phosphoglucose Isomerase	a					.22	.38	
	b	1.00	1.00	.99	1.00	.75	.62	.88
	c			.01				
	d					.02		.12
Lactate Dehydrogenase-1	a						.04	
	b					.92	.96	1.00
	c	1.00	1.00	1.00	1.00			
	d					.08		
Lactate Dehydrogenase-2	a							.12
	b	1.00	1.00	1.00	1.00	1.00	1.00	.88
Isocitrate Dehydrogenase-1	a					1.00	1.00	1.00
	b		.04					
	c	1.00	.77	.95	.85			
	d		.19	.05	.15			
Malate Dehydrogenase-1	a							.12
	b	1.00	1.00	1.00	1.00	1.00	1.00	.88
Malate Dehydrogenase-2	a		.12					
	b	1.00	.98	1.00	1.00	1.00	1.00	1.00
Alcohol Dehydrogenase	a					.12	.04	.12
	b	1.00	1.00	1.00	1.00			
	c					.88	.96	.88
Glutamic Oxaloacetic Transaminase-1	a	1.00	1.00	.99	1.00	1.00	1.00	1.00
	b			.01				
6-Phosphogluconate Dehydrogenase	a							.62
	b	.06				1.00	1.00	
	c							.38
	d	.94	.98	1.00	1.00			
	e		.02					
Phospho-glucomutase-1	a	1.00	1.00	1.00	1.00			
	b					1.00	.92	1.00
	c						.08	

Table 1 — Continued

Phospho-glucomutase-2	a	.06		.07				
	b	.83	.83	.83	.85	.92	.81	1.00
	c					.02	.19	
	d	.11	.17	.10	.15			
	e					.05		
Peptidase	a	.17						
	b	.83	1.00	1.00	1.00			
	c					1.00	1.00	1.00
Fumarase	a					.02	.12	
	b	1.00	1.00	.99	1.00	.98	.88	1.00
	c			.01				
Indophenol Oxidase	a			1.00				
	b					1.00		
Hemoglobin	a			1.00				
	b					1.00		
Plasma Protein-1	a			1.00				
	b					1.00		

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[1] Proteins B and C, leucine aminopeptidase, isocitrate dehydrogenase-2, α-glycerophosphate dehydrogenase, and glutamic oxaloacetic transaminase-2 were invariant.

[2] Electrophoretic mobility determines order in lists of variants, with 'a' the most distant from the origin.

Table 2. Normalized identity of genes (*I*) as computed from 21 genes for all pairs of samples.

Sample Number	2	3a	3b	4a	4b	5
1	.996	.998	.997	.622	.611	.624
2		.998	.999	.618	.608	.623
3a			.999	.614	.604	.619
3b				.617	.606	.622
4a					.996	.958
4b						.951

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EVOLUTION AND CLASSIFICATION OF PLACODERM FISHES

Robert H. Denison

Abstract. The assumption is made that within the Subclass Placodermi a shoulder girdle that is short anteroposteriorly is primitive. Most orders retaining this feature show distinctive specializations: thus the Rhenanida are ray-like, the Ptyctodontida are chimaeroid-like, the Pseudopetalichthyida have large, dorsal eyes, and many Acanthothoraci have dorsal nostrils. The Stensioellida show few specializations are are believed to be the most primitive known Placodermi, yet they possess the three characters that distinguish the subclass: 1) gills anteriorly placed under the neurocranium; 2) a neck joint between the neurocranium and synarcual; and 3) dermal bones. The primitively short shoulder girdle becomes lengthened to form a thoracic shield in several stages. Some Acanthothoraci add posterior lateral and posterior dorsolateral plates. The Petalichthyida add a long ventral shield. Primitive Arthrodira lengthen the lateral shield and close it behind the pectoral fins which then attach through fenestrae. Finally, the Antiarcha develop a long, boxlike shield and transform the spinal plates into peculiar pectoral appendages. A phyletic classification of Placodermi is attempted.

INTRODUCTION

The Placodermi are a suborder of fishes whose known history is practically restricted to the Devonian period unless, as some think, they were ancestral to the chimaeroids. During that relatively short time span they underwent a considerable radiation and gave rise to 34 families and about 170 genera. In recent years they have been the subject of considerable research by many paleontologists. Yet, in spite of a great advance in our knowledge of the group, there is still little agreement about their evolutionary history and classification. This results from widely different assumptions about what constitutes primitive or derived characters within the group. Gross (1954) argued that an elongated thoracic shield such as occurs in early Arthrodira is primitive, and the well-documented reduction of this shield within Arthrodira may be adduced to support this. Westoll (1945) likewise placed the long-shielded "Arctolepida" at the base of his placoderm phylogeny, and Miles (1969) has concluded that the formation of a firm thoracic shield, together with the development of a neck joint, was the fundamental placoderm adaptation. On the other hand, Stensiö in various works (e.g., 1969–1971) has based his classification primarily on the pectoral fin and endoskeletal shoulder girdle; following the fin-fold theory of paired fin origins, he believes that the primitive state is long-based pectoral fins together with an elongated endoskeletal shoulder girdle for their articulation.

CHARACTERS OF PRIMITIVE PLACODERMI

In my opinion, neither of these theories is correct, and my classification and phylogeny is based on the assumption that within the Placodermi an anteroposteriorly short shoulder girdle is primitive. The justification for this assumption is the fact that a short exoskeletal shoulder girdle occurs in all other groups of fishes with bony exoskeletons, and a short scapulocoracoid is characteristic of Chondrichthyes. It is only in certain groups of Placodermi, the Petalichthyida, Arthrodira, Phyllolepida and Antiarcha, that the exoskeletal shoulder girdle is elongated to form a thoracic shield, and this can be taken as an indication that it is a derived state within Pisces and within Placodermi as well. On the assumption, then, that a short shoulder girdle is primitive within Placodermi, we may look at the groups that possess this character for other primitive states. The classification used in this discussion is given in the appendix, and is indicated pictorially in the phylogenetic chart (Fig. 6); some parts of it will be discussed later.

The following orders have a short exoskeletal shoulder girdle:

Stensioellida (*Stensioella*)
Rhenanida (*Gemuendina, Asterosteus, Ohioaspis, Jagorina*)
Pseudopetalichthyida (*Pseudopetalichthys, Paraplesiobatis*)
Acanthothoraci (*Palaeacanthaspis, Kosoraspis, Radotina, Kolymaspis, Kimaspis*)
Ptyctodontida (8 genera)

All of these orders appear in the Lower Devonian; they show the following characters which may be primitive:

Thoracic region.

1) The ventral shoulder girdle (Figs. 1–2, sh) consists of a single pair of plates homologous either to the interolaterals or anterior ventrolaterals of Arthrodira; between them a median plate has been identified only in Ptyctodontida.

2) The lateral shoulder girdle consists only of anterior laterals and anterior dorsolaterals, except in some Acanthothoraci (Fig. 1C) where posterior laterals and posterior dorsolaterals are also present.

3) The spinal plates are absent, or small and doubtfully distinct, except in Acanthothoraci and some Ptyctodontida (Fig. 1C–D, Sp).

4) A median dorsal plate is probably absent in Stensioellida and Pseudopetalichthyida.

5) Pectoral fins are narrow-based, even in Rhenanida where the fins are much expanded distally (Fig. 1B).

6) There is no exoskeletal craniothoracic joint, except in Ptyctodontida where it is developed differently than in Arthrodira and Antiarcha.

7) The anterior vertebrae are fused to form a synarcual (Figs. 1–2, syn) which articulates with the occipital region of the neurocranium (not known in Acanthothoraci).

Skull.

8) The neurocranium is long and slender with a long occipital region, except in Ptyctodontida where it must have been short.

9) The dermal cranial roof bone pattern may be variable and unstable with relationships between bones and sensory canals not firmly established, except in Ptyctodontida.

10) Dermal cranial roof bones may be small and part of the roof may be covered with thin, superficial tesserae in Acanthothoraci (Fig. 3, te) and Rhenanida; much of the skull in Stensioellida (Fig. 2A) is covered with denticles or tesserae; the central part of the cranial roof of Pseudopetalichthyida is covered with small dermal bones, but there may have been denticles or tesserae elsewhere. Denticles or tesserae are unknown in Ptyctodontida, but may have covered the snout and cheeks where dermal bones are largely absent (Fig. 1D).

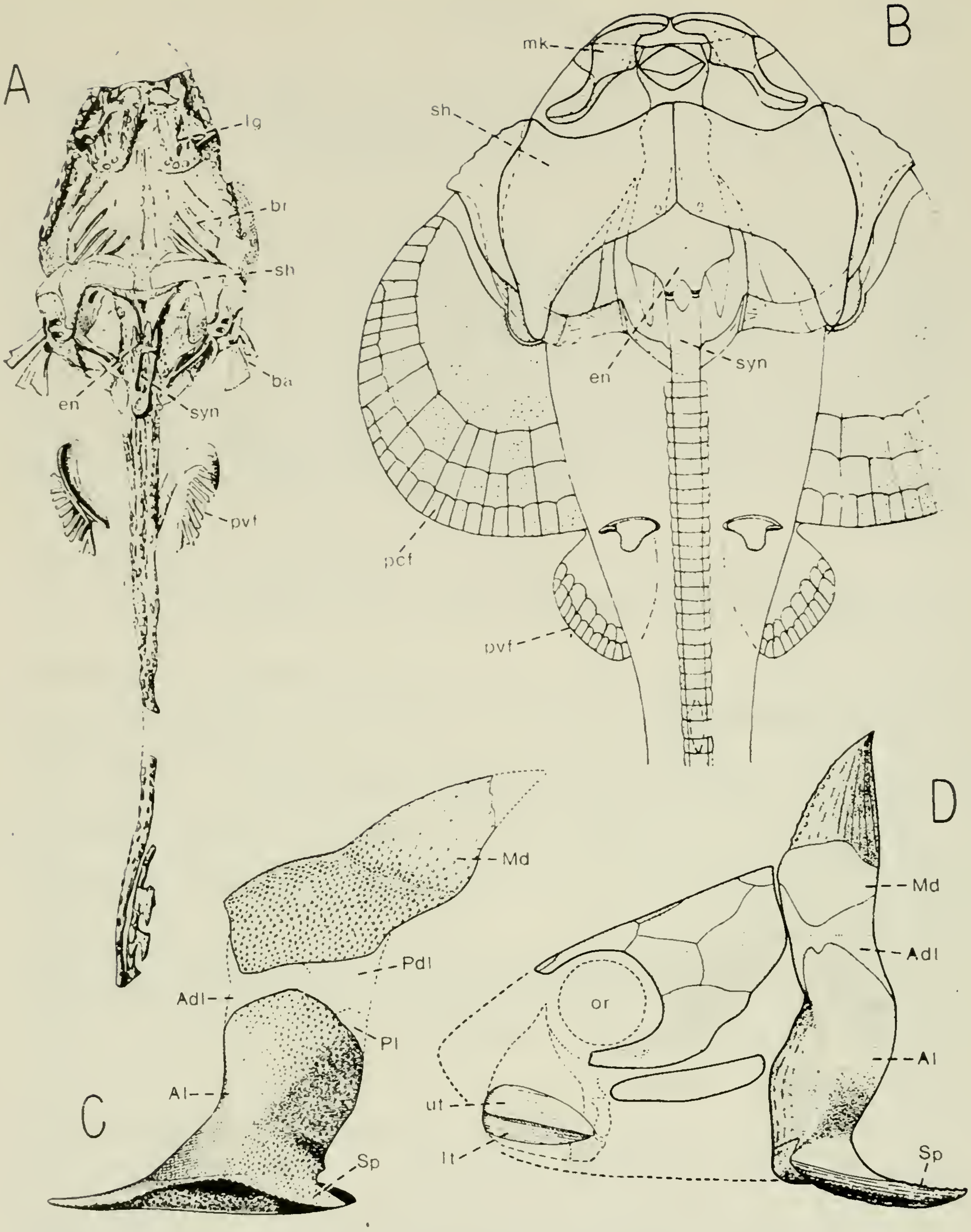


Figure 1. Placodermi with short shoulder girdles: A, Order Pseudopetalichthyida (ventral view of *Pseudopetalichthys problematica,* ×0.66, from Gross, 1962) ; B, Order Rhenanida (ventral view of *Gemuendina stuertzi,* ×0.60, from Gross, 1963) ; C, Order Acanthothoraci (lateral view of shoulder girdle of *Palaeacanthaspis vasta,* ×0.94, from Stensiö, 1944) ; D, Order Ptyctodontida (lateral view of head and shoulder girdle of *Rhamphodopsis threiplandi,* ×2.5. from Miles, 1967) . Adl, anterior dorsolateral plate; Al, anterior lateral plate; ba, basal elements of pectoral fin; br, branchial arches; en, endocranium; lg, lower jaw; lt, lower dental plate; Md, median dorsal plate; mk, Meckel's cartilage; or, orbit; pcf, pectoral fin; Pdl, posterior dorsolateral plate; Pl, posterior lateral plate; pvf, pelvic fin; sh, shoulder girdle; Sp, spinal plate; syn, synarcual; ut, upper dental plate.

Jaws and Gills.

11) The jaws, where known, are more or less transverse and lack large dermal elements (Fig. 1A-B, 2B), except in Ptyctodontida where they are directed more anteroposteriorly and carry large crushing or sectorial tooth plates (Fig. 1D, ut, lt).

12) Gill covers (submarginals) may be present, though they are not known in Acanthothoraci and their dermal bones are small in Ptyctodontida.

Sensory organs.

13) The orbits are small and lateral in Stensioellida and most Acanthothoraci, large and dorsolateral in Ptyctodontida, and dorsal in Pseudopetalichthyida, Rhenanida and one late genus of Acanthothoraci; the last condition is surely specialized.

14) The nostrils are known only in Rhenanida and Acanthothoraci (Fig. 3, no) where they are usually dorsal, a condition that is surely specialized. In Stensioellida, Pseudopetalichthyida and primitive Acanthothoraci they are presumed to be anterior or anteroventral; there are no clues to their position in Ptyctodontida.

Body and fins.

15) The body is depressed and tapers to a diphycercal tail (not known in Acanthothoraci).

16) Dorsal fins are little developed except in Ptyctodontida; there are dorsal ridge scales in Pseudopetalichthyida (Fig. 1A) and Stensioellida and the latter has a small dorsal fin (Fig. 2A, df) at the base of the tail; an enlarged ridge scale forms a small dorsal spine in Rhenanida. (This region is not known in Acanthothoraci.)

17) Pelvic fins (Figs. 1–2, pvf) are long-based and semicircular in Rhenanida, Stensioellida and Pseudopetalichthyida; they are specialized by the development of claspers in male Ptyctodontida.

Histology.

18) The histology of the Lower Devonian members of the groups under discussion is practically unknown. There is a possibility that the Stensioellida had denticles composed of dentine, and if so, this would be the only occurrence of this tissue in Placodermi except for the tooth plates of Ptyctodontida. Typically in other Placodermi the superficial layer is reduced and the external part of dermal bones is composed of semidentine or bone.

PRIMITIVENESS OF PLACODERM ORDERS WITH SHORT SHOULDER GIRDLES

In reviewing the list of probable primitive characters, it is clear that the Ptyctodontida (Fig. 1D) do not share many of them. This may be due to the fact that only the shoulder girdle is known in Lower Devonian ptyctodonts while other characters are determined from Middle or Upper Devonian genera which are specialized or advanced in the following ways: the presence in the shoulder girdle of an anterior medioventral, a median dorsal, spinal plates in some, and an exoskeletal craniothoracic joint; in the shortness of the exo- and endocranium, well-established cranial roof pattern without tesserae (except perhaps anteriorly and on the cheeks), large dorsolateral eyes, large dermal jaw elements, firm attachment of palatoquadrate to endocranium, dorsal fins, and pelvic fins with claspers in males.

It is clear that the ray-like Rhenanida (Fig. 1B) are also specialized, even in the earliest known Lower Devonian forms. They have a much flattened body, greatly expanded pectoral fins, dorsal eyes and nostrils, a median dorsal plate, and a dorsal spine on the body.

The Acanthothoraci, with the exception of the Radotinidae, are advanced in having the lateral parts of the shoulder girdle lengthened by the addition of posterior lateral and posterior dorsolateral plates (Fig. 1C); well-developed, projecting spinal plates as well as median dorsal plates are present. The skull in all members of the order is distinguished by its narrow proportions, subparallel sides, and deeply embayed posterior margin with strongly projecting paranuchals. Primitively, (Palaeacanthaspidae) the eyes were lateral and the nostrils probably ventral, but the nostrils, or both the nostrils and eyes have moved to the dorsal side in Radotinidae (Fig. 3) and Kolymaspidae, both of which have a prominent rostrum.

The poorly known Pseudopetalichthyida (Fig. 1A) are surely specialized in their relatively large, dorsal eyes, the long preorbital region, and possibly in the absence of tesserae, at least on the cranial roof. Their jaws (Fig. 1A, lg), though not well understood, appear to be peculiarly specialized.

This leaves only the Stensioellida, which exhibit very few characters that can be interpreted as advanced, and are considered to be the most primitive Placodermi known, even though they are not the earliest members of the subclass. Based on the two specimens of *Stensioella* (Fig. 2) from the Hunsrückschiefer of Germany, the body appears to be somewhat depressed, broadest in the head and shoulder regions, and tapering backwards towards the tail. Flattening after burial spread apart the two halves of the shoulder girdle (Fig. 2, sh), making it difficult to

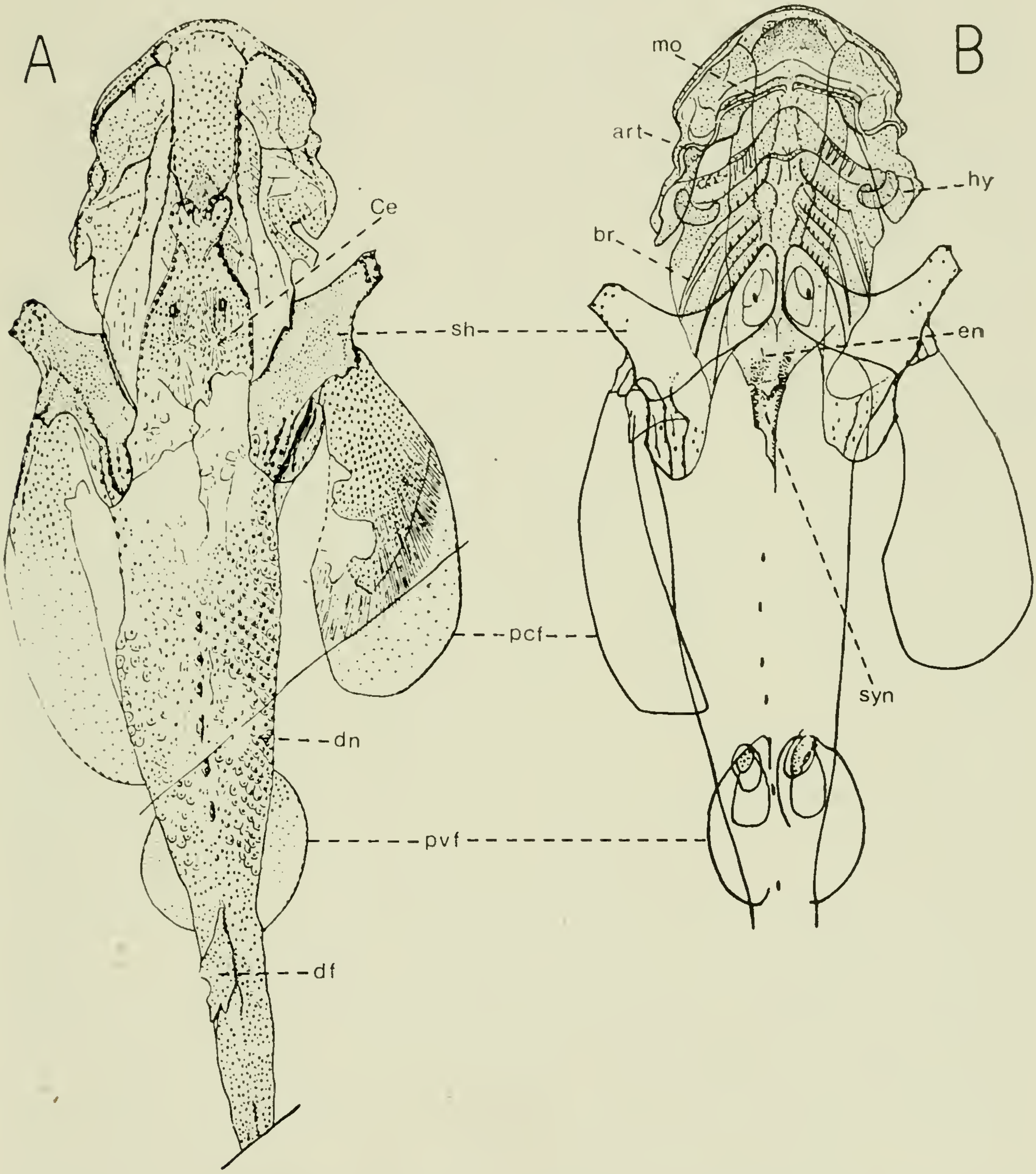


Figure 2. *Stensioella heintzi* (the only known reprepresentative of the Order Stensioellida), ×0.44, from Gross, 1962: A, dorsal; B, ventral. art, jaw articulation; br, branchial arches; Ce, central plate; df, dorsal fin; dn, denticles; en, occipital region of endocranium; hy, hyomandibular; mo, mouth; pcf, pectoral fin; pvf, pelvic fin; sh, shoulder girdle; syn, synarcual.

interpret, but the bones are tuberculate and thus largely exoskeletal, even though individual dermal bones cannot be identified. Clearly the shoulder girdle is short anteroposteriorly, lacks a median dorsal and median ventral, and has no large or projecting spinal plates. Each half of the shoulder girdle has an inner or medial lamina which forms a postbranchial wall; such a wall occurs in many placoderms, but is absent in primitive Arthrodira, so this may well be an advanced character in *Stensioella.* The pectoral fins (Fig. 2, pcf) are narrow-based, scale-covered and with ceratotrichia distally, but their inner skeleton is unknown. There is no exoskeletal craniothoracic joint, but apparently there is a synarcual formed of fused anterior vertebrae (Fig. 2, syn) that articulates with the occipital region of the endocranium. The body is covered with denticles (Fig. 2, dn) which possibly have pulp cavities and thus perhaps were composed of dentine, and possibly, though not certainly, were attached to thin tesserae. There are long-based, semicircular pelvic fins (Fig. 2, pvf), and a small, delicate dorsal fin (Fig. 2, df) at the base of the tail, the termination of which is unknown.

Judging from its manner of preservation, the head and body were depressed dorsoventrally, but only moderately broad. The neurocranium must have been long and relatively slender, but was poorly ossified, except in the occipital region where an articulation was developed for the synarcual (Fig. 2, en). The dermal covering of the head was largely denticles, possibly attached to tesserae, but there are at least three small bones with radiating structure — a median postpineal and paired centrals (Fig. 2A, Ce). The orbits have not been seen, but must have been lateral, and the nostrils do not appear on the dorsal surface of the head so are assumed to be anterior or anteroventral. The supraorbital sensory canals are bounded by large tubercles and are presumably quite superficial; from the snout they run subparallel back to the middle of the skull. Posterior pit lines are shallow grooves on the central plates. The mouth (Fig. 2B, mo) is ventral, but only a short distance behind the rostrum. The palatoquadrates and Meckel's cartilages carry no dermal jaw bones, only small denticles. As interpreted by Gross (1962), the jaw suspension was hyostylic, but this is not certain. There appear to be five branchial arches (Fig. 2B, br) and these extend far anterior under the endocranium.

The single species that constitutes the Order Stensioellida has many characters that are considered primitive within the placoderms, but shows no easily identifiable specializations or unique derived characters that can be used to distinguish it from other placoderm orders. Nonetheless, it seems to be a distinct order occupying an isolated position as an offshoot from the base of the placoderm stem.

DIAGNOSTIC CHARACTERS OF PLACODERMS

That Stensioellida are placoderms is indicated by their possession of three characters: 1) the gills lie far forward under the neurocranium; 2) there is a neck joint between the endocranium and synarcual; and 3) there are dermal bones on the head and shoulder girdle. The first two characters are shared by the Holocephali which may support, though it does not establish, their postulated relationship to Placodermi. But the possession of all three features is unique to Placodermi, and for that reason their significance requires further consideration.

Miles (1967, 1969) attempted to show that the neck joint arose to compensate for the rigidity of the anterior part of the body when it became enclosed within a thoracic shield. However, this joint occurs in the placoderm orders discussed above which have a short shoulder girdle and no rigid thoracic armor. The same is true in chimaeroids so one may question whether it was the evolution of a stiff armor that led to the development of the neck joint. The joint permits largely vertical movement between the head and shoulder girdle and functions in three main ways (Miles, 1967): 1) to aid in locomotion by control of pitching equilibrium; 2) to aid in feeding by permitting a wider gape and by helping to force food into the esophagus; and 3) to aid in respiration by forcing water through the gills. The first was probably of only minor importance to early placoderms which were slow-swimming, benthonic forms. The second may have been important to some later, predaceous placoderms, but the early ones had small mouths and surely ate small food that did not require a wide gape. However, the neck joint may have been necessary for respiration when the gills became crowded under the neurocranium; then, a raising and lowering of the head would help to force a stream of water through the gills. Thus the neck joint may have been related to the anterior position of the gills under the head; instead of being a response to the rigidity of the thoracic region, it may have permitted the later development in some groups of a stiff trunk armor.

Dermal bones are characteristic of Placodermi, and typically a superficial layer of dentine is absent and their surface is formed of semidentine or bone. In the Lower Devonian groups with a short shoulder girdle, specimens are either unavailable or unsuitable for histologic study so superficial tissues have not been identified. Primitive or ancestral Placodermi might be expected to retain dentine in teeth, denticles or tubercles, and Gross (1962) has recognized what may be pulp cavities in the denticles of *Stensioella,* suggesting that they were made of dentine. Lower Devonian Rhenanida have not been studied histologically, but the Middle Devonian members have semidentine superficially. Ptyctodontida have dentine in their tooth plates (Ørvig, 1957), the only occurrence of this tissue in later Placodermi.

The problem of dermal bone origins in placoderms is complicated by the presence of tesserae in certain groups — the Rhenanida, Acanthothoraci, Lower Devonian Petalichthyida, and possibly Stensioellida. Since tesserae occur mostly in early

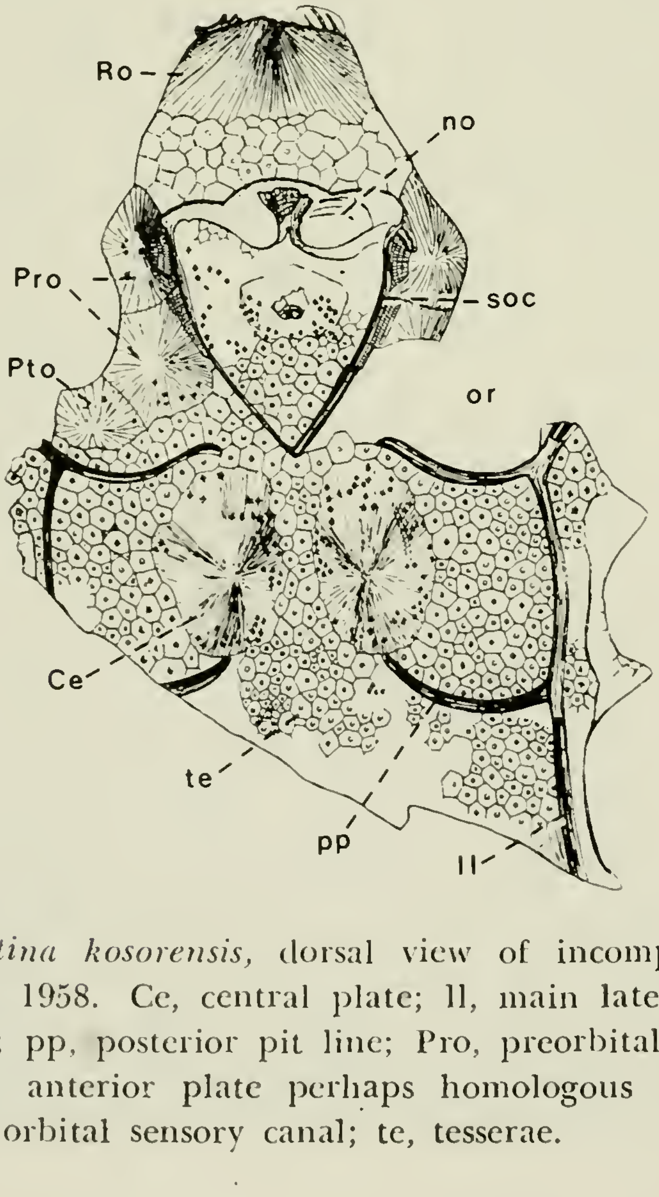


Figure 3. *Radotina kosorensis,* dorsal view of incomplete cranial roof, ×0.9, from Gross, 1958. Ce, central plate; ll, main lateral line; no, nasal opening; or, orbit; pp, posterior pit line; Pro, preorbital plates; Pto, postorbital plate; Ro, anterior plate perhaps homologous to rostral or premedian; soc, supraorbital sensory canal; te, tesserae.

forms, they are probably a primitive character, as has been maintained by Gross (1959). He has shown in *Radotina* (Fig. 3, te) that tesserae are thin, superficial structures that occur for the most part between bones, and that do not fuse together to form bones or even their superficial parts. In Rhenanida they are homologous to the scales that cover the body (Gross, 1963). They may be considered remnants of the dermal scales that were the only exoskeleton of ancestral placoderms, and as such are comparable in general to chondrichthyan scales. When bones first appeared in placoderms, they apparently arose deeper in the dermis quite independently of the tesserae and also of the lateral line system. The depth of their formation may account for the absence of any true dentine on the bones of typical Placodermi, and also for the fact that the course of the lateral line canals in Rhenanida and Acanthothoraci is not dependent on the dermal bones. Presumably the close relationship between the dermal bones and lateral line canals was secondary and, as suggested by Parrington (1949), the precursors of dermal bones may later have come to influence the direction of growth of lateral line primordia.

The pattern of dermal bones on the skull differs in the various groups of Placodermi yet shows enough similarities to suggest that, in most cases at least, it was derived from a common ancestral pattern. In Stensioellida the pattern is hardly developed for in the cranial roof there is only a median bone identified as a postpineal and paired bones that resemble centrals (Fig. 2A, Ce). Likewise in the Lower Devonian Rhenanida the cranial roof largely lacks dermal bones, though laterally there are suborbitals, submarginals and possibly paranuchals. In all other groups, except perhaps the poorly known Pseudopetalichthyida, the skull bones are developed according to a similar pattern. This pattern includes some or all of the following: 1) median nuchal, postpineal, pineal and rostral; 2) paired centrals over the otic region; 3) paired paranuchals and marginals carrying the main lateral line forward; 4) paired pre- and postorbitals over the orbits; 5) paired postnasals beside the nostrils; and 6) paired suborbitals, postsuborbitals, postmarginals and submarginals in the cheek and opercular region. Much of this pattern is becoming established in the Acanthothoraci (Fig. 3), while in Ptyctodontida, Arthrodira, Phyllolepida and Antiarcha there are relatively stable cranial bone patterns, though with characteristic modifications in the various subgroups (Figs. 4–5).

PHYLETIC HISTORY OF PLACODERMI

In my theory of placoderm evolution, as presented pictorially in the phylogenetic chart (Fig. 6), particular emphasis is given to the dermal shoulder girdle. This remains short in Stensioellida, Pseudopetalichthyida, Rhenanida and Ptyctodontida, while the first steps towards lengthening it to form a thoracic shield are seen in some Acanthothoraci (Palaeacanthaspidae and Kolymaspidae), where posterior laterals and posterior dorsolaterals are added (Fig. 1C, Pl, Pdl). The second stage is the development of a ventral shield composed, in addition to interolaterals, of anterior and posterior ventralaterals and anterior and posterior medioventrals; this is seen in Petalichthyida and Arthrodira. Early members of the latter group go one step further in uniting the posterior parts of the ventral and lateral shields behind the pectoral fins to enclose pectoral fenestrae (Fig. 5B-F, pf). The Antiarcha have the longest thoracic shield and have a posterior median dorsal incorporated in it (Fig. 5K, Pmd).

There are three major phylogenetic problems that require special mention, the first involving the Petalichthyida (Fig. 5A). Their thoracic shield might have evolved quite independently from that of Arthrodira, in which case a relationship to Pseudopetalichthyida should be considered. However, since the latter group is so poorly known and the petalichthyid thoracic shield is so similar to that of Arthrodira, this theory has little to recommend it. Secondly, the petalichthyid thoracic shield may have arisen as a result of a posterior reduction of the lateral parts of the arthrodire shield. There is no evidence to support this, and in fact it is quite unlikely that the petalichthyid cranial roof was derived from the arthrodire type, so this theory is rejected. The third theory is that the petalichthyid thoracic shield represents an intermediate evolutionary stage, more advanced than in Acanthothoraci in the possession of a ventral shield, but less advanced than early Arthrodira as the pectoral fins are completely behind the shield. This theory seems most probable and is supported by the retention of certain primitive characters in Petalichthyida, such as the two pairs of paranuchals and tesserae on the cheeks.

The evolutionary position of *Phyllolepis* (Fig. 4) is also controversial because, though it has a moderately long thoracic shield, it lacks posterior laterals and posterior dorsolaterals. Is the absence of these plates the result of a phyletic reduction, or did *Phyllolepis* branch off the arthrodiran ancestral line before

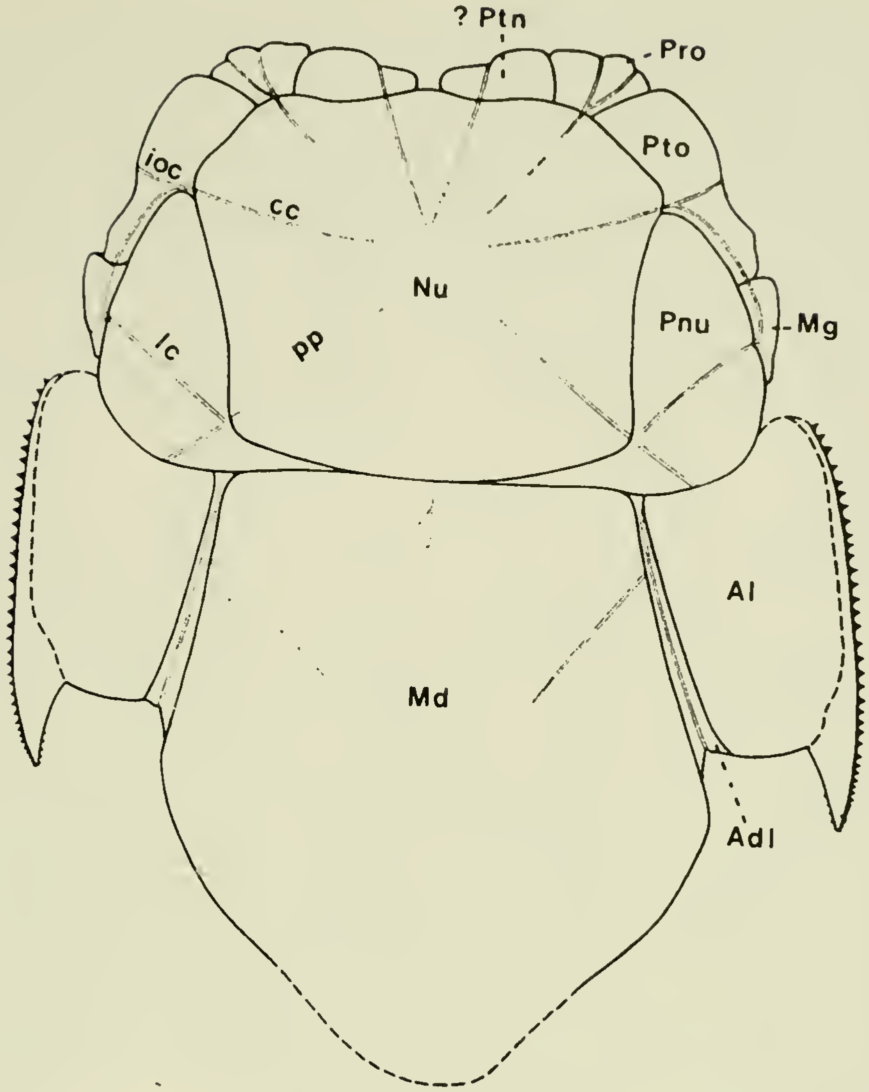


Figure 4. *Phyllolepis orvini,* dorsal view of cranial and thoracic shields, ×0.2, modified from Stensiö, 1936. Adl, anterior dorsolateral plate; Al, anterior lateral plate; cc, central sensory canal; ioc, infraorbital sensory canal; lc, main lateral line; Md, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; Pnu, paranuchal plate; pp, posterior pit line; Pro, preorbital plate; ? Ptn, possible postnasal plate; Pto, postorbital plate.

these plates were acquired? Since this genus is known only from the late Famennian there is little evidence to decide this question. However, the genus *Antarctaspis,* known only from an imperfect cranial roof, seems in some ways to bridge the gap between *Phyllolepis* and primitive Actinolepina, which suggests that Phyllolepina were derived from the latter by a reduction of the thoracic shield, and, of course, by considerable modification of the cranial roof.

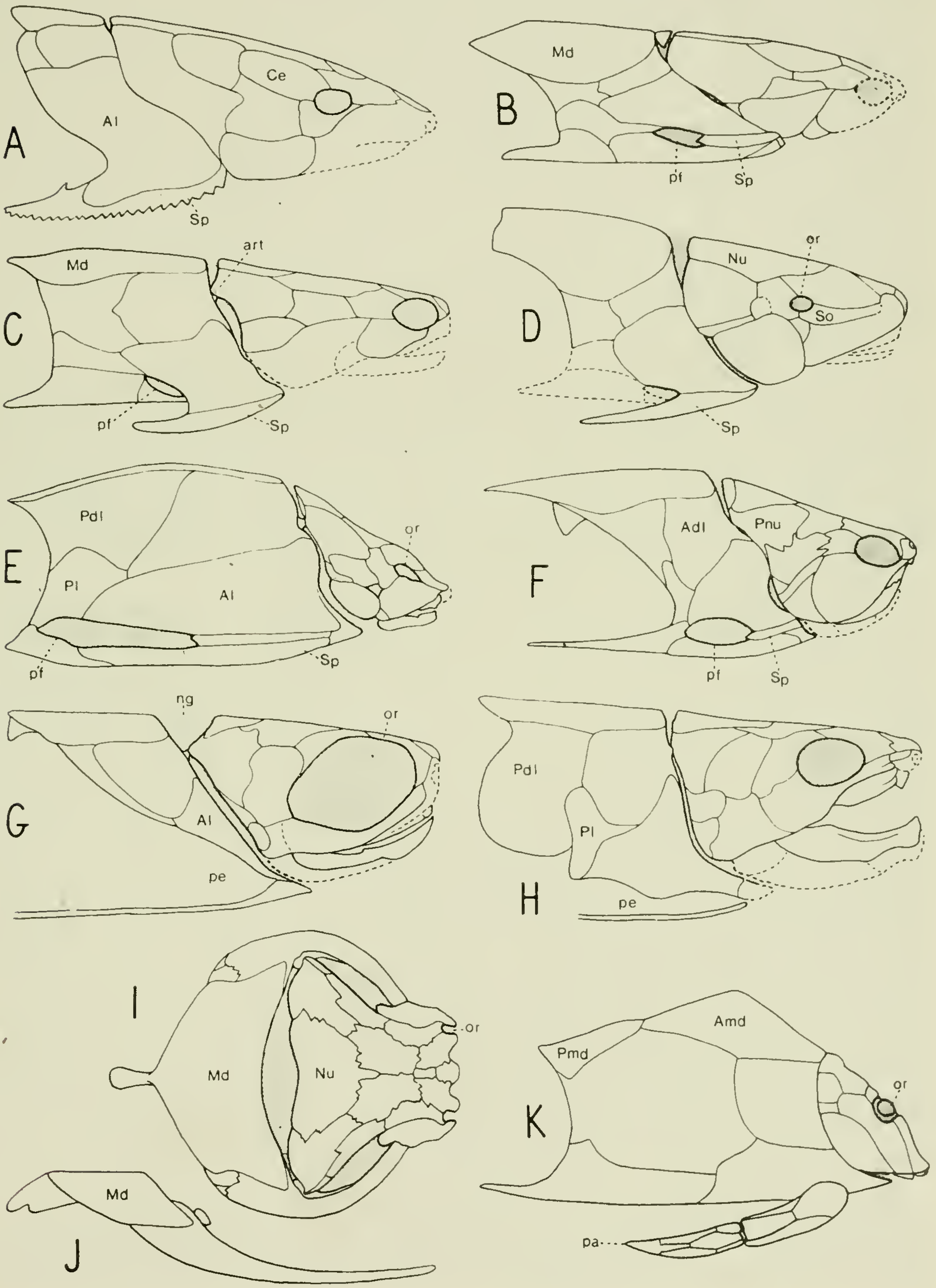
The Ptyctodontida (Fig. 1D) are a third phyletic problem. If it is accepted that their short dermal shoulder girdle is a primitive character and not the result of reduction, they cannot be derived from Arthrodira, Petalichthyida or some Acanthothoraci.

Yet in their dermal cranial bones they show many resemblances to these groups, so they probably had an ancestor with a short shoulder girdle and the basic placoderm cranial bone pattern. The Radotinidae are the only known group that satisfies these conditions, but because of their elongated skull and dorsal nostrils (Fig. 3, no), their relationship to Ptyctodontida will be questioned, particularly by those who believe the ptyctodonts were ancestral to chimaeroids. However, it must be pointed out that nothing is known about the position of the nostrils in ptyctodonts.

The Order Arthrodira is the best known and most varied group, including currently 121 genera or 72% of known placoderm genera, yet the classifications that have been proposed for it have been largely by level of organization, rather than phylogenetic. This is true of the commonly used major subdivisions, the Arctolepida (or Dolichothoraci) and Brachythoraci (and its two subgroups, the Coccosteomorphi and Pachyosteomorphi). It appears to be worthwhile to attempt a phyletic classification, even though our incomplete knowledge will make this provisional and certainly subject to future corrections and additions. Instead of the two to four gradal subdivisions of current usage, the 21 arthrodiran families are grouped according to their probable common ancestry in 8 suborders.

Figure 5. Cranial and thoracic shields of Placodermi with elongated shoulder girles, lateral views except I. A. Order Petalichthyida (*Lunaspis heroldi,* after Stensiö, 1963) ; B, Suborder Actinolepina (*Sigaspis lepidophora,* after Miles, 1973) ; C, Suborder Phlyctaeniina (*Phlyctaenius acadica,* after Heintz, 1934 and Westoll and Miles, 1963) ; D, Suborder Wuttagoonaspina (*Wuttagoonaspis fletcheri,* attempted restoration based on figures of Ritchie, 1969 and 1973) ; E. Suborder Holonematina (*Holonema westolli,* after Miles, 1971) ; F, Suborder Coccosteina (*Coccosteus cuspidatus,* after Miles and Westoll, 1968) ; G, Suborder Pachyosteina (*Rhinosteus parvulus,* after Stensiö, 1963) : H, Suborder Brachydeirina (*Leptosteus bickensis,* after Stensiö, 1963) ; I-J, Suborder Heterostiina (*Heterostius ingens*) ; I, dorsal view of cranial and thoracic shields, after Heintz, 1929; J, lateral view of thoracic shield, after Heintz, 1929; K, Order Antiarcha (*Pterichthyodes milleri,* after Traquair, 1914) . Adl, anterior dorsolateral plate; Al, anterior lateral plate; Amd, anterior median dorsal plate; art, cranio-thoracic joint; Ce, central plate; Md, median dorsal plate; ng, nuchal gap; Nu, nuchal plate; or, orbit; pa, pectoral appendage; Pdl, posterior dorsolateral plate; pe, pectoral emargination; pf, pectoral fenestra; Pl, posterior lateral plate; Pmd, posterior median dorsal plate; Pnu, paranuchal plate; So, suborbital plate; Sp, spinal plate.

The first suborder to appear and surely the most primitive is the Actinolepina (Fig. 5B), with a single family, the Actinolepidae. It has the elongated thoracic shield that typifies early Arthrodira, and it is closed behind the pectoral fins to form pectoral fenestrae (Fig. 5B, pf), as is characteristic of primitive members of the order. The spinal plates are well developed and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projecting but not greatly elongated (Fig. 5B, Sp), the pectoral fins are narrow-based, the median dorsal short and broad (Fig. 5B, Md), the endocranium platybasic, the orbits small and anterior, and the rostral region containing the nasal capsules sometimes separately ossified. All of these characters are primitive within Arthrodira, though some are advanced for Placodermi. However, Actinolepina are distinguished from other Arthrodira by one feature that is clearly derived: there is a sliding joint between the cranial and thoracic shields formed by smooth, anterior flanges on the anterior dorsolaterals that are overlapped by the underside of the paranuchals. No doubt there were a number of phyletic lines within the Actinolepidae; one of them, represented by *Baringaspis* and *Aethaspis,* shows a tendency to reduce the centrals and elongate the nuchal, sometimes by fusion with the postpineal. It is from this line that the Antarctaspidae and Phyllolepidae may have been derived.

Another line retained a typical actinolepid thoracic shield with a sliding craniothoracic joint (if Ritchie's 1969 restoration is correct), yet modified the cranial roof so greatly that it has been placed in its own suborder, the Wuttagoonaspina (Fig. 5D). The cranial modifications resulted from great enlargement of the nuchal plate and a migration of the eyes backwards.

Though Miles has recently (1973) expressed a contrary opinion, it seems probable that in some Actinolepidae the sliding type of neck joint evolved into a more complicated and efficient ginglymoid articulation, with condyles developed on the anterior dorsolaterals and glenoid fossae on the paranuchals. It is the acquisition of this joint (Fig. 5C, art) that particularly distinguishes the Phlyctaeniina from their ancestors among the Actinolepina, and the joint is retained, with one exception, in all the many descendants of the Phlyctaeniina. The dominant family, the Phlyctaeniidae, showed a tendency to elongate the median dorsal plate (Fig. 5C, Md), though one genus retained the short, broad type of Actinolepidae, and many of the known genera became specialized in their excessively long spinal plates (Fig. 5C, Sp). The Williamsaspidae may be a differently specialized side-branch of Phlyctaeniina, but this is uncertain since their skull and dorsal part of the thoracic shield is unknown.

An early and distinctive branch from the Phlyctaeniina is the Holonematina with the single family Holonematidae (Fig. 5E). Their skulls are distinguished by the large pineal plate lying between the preorbitals, the orbits that deeply notch the cranial roof, and the moderately small, subtriangular nuchal. The thoracic shield remains long or is even lengthened, and retains the contacts between the lateral and ventral shields behind the pectoral fins. The anterior laterals (Fig. 5E Al) tend to lengthen, crowding the pectoral fins backwards. The posterior laterals are large (Fig. 5E, Pl), and there is a large anterior medioventral. Characteristically the main lateral line extends towards the posteroventral corner of the anterior dorsolateral and has a strong flexure on the posterior dorsolateral. Primitive members of the suborder have previously been referred to the Groenlandaspididae which, until the recent discoveries of Ritchie (1974), have been of uncertain affinities.

The Suborder Coccosteina (Fig. 5F), the most important derivative of the Phlyctaeniina, may be recognized by the nuchal plate which is trapezoidal in shape and widened posteriorly, by the paranuchals which are narrow posteriorly except for strong postnuchal processes, and by the centrals which tend to be divided into anterior, lateral and posterior lobes. The orbits typically are directed more laterally than in Phlyctaeniidae, and the pineal comes to lie posteriorly between the preorbitals. In the thoracic shield, the median dorsal, which is primitively rather long, tends to be shortened; the pectoral fenestrae are lengthened though usually remain closed posteriorly (Fig. 5F, pf). The spinals tend to be reduced (Fig. 5F, Sp), and the ventral shield is typically lengthened. These characters are well displayed by the Family Coccosteidae, which is also distinguished by the postbranchial laminae projecting from the mesial faces of the anterior laterals, by the course of the main lateral lines parallel to the ventral exposed edges of the anterior dorsolaterals, and by the long, slender suborbital processes of the suborbital plates. The Gemuendenaspidae show their relationship to the Coccosteina in the shape of the dermal bones of the posterior part of the cranial roof, but retain a number of primitive characters, such as the broad, depressed shield, the long, narrow median dorsal, and the short, deep suborbital processes on the suborbital plates. The Buchanosteidae also have the characteristic nuchal and paranuchal plates of Coccosteina, but show a peculiar mixture of primitive and specialized characters: they are primitive in not having the rostral capsule fused to the rest of the skull, in the forwardly directed orbits, in the short, deep suborbital processes, and in the short, wide preorbitals; but they are distinctively specialized in the long postmarginals, the unusually shaped anterior laterals which bend inwards to form postbranchial laminae, and in the short, nonprojecting spinals. A specialized family known only in the Frasnian, the Pholidosteidae, is distinguished by its enlarged eyes and elongated orbitotemporal region, by having the cheek bones rigidly sutured to the cranial roof, and by their long, laterally projecting spinal plates carried by protruding wings of the anterior laterals and anterior ventrolaterals. This family must have diverged early from the Coccosteidae before the reduction of the spinals. The Homostiidae (including both typical Homostiidae and Euleptaspidae) show a relationship to the Coccosteina in the characteristically shaped nuchal, paranuchals, and centrals, and their appearance in the Siegenian suggests an origin from early members of the suborder. The family includes large forms with a broad, depressed head and body, and is characterized particularly by the great elongation of the bones of the posterior half of the cranial roof. The advanced Homostiidae are highly specialized in the dorsal position of the eyes and in the great shortening of the thoracic shield, but retain some primitive characters such as a narrow nuchal gap and tuberculated dermal bones. Finally, the Rachiosteidae are shown to be Coccosteina by the shape and proportions of the nuchal, paranuchals and centrals, but have reduced the lateral and ventral thoracic shields even more than in some advanced Pachyosteina, and have also lost the ornamentation on their dermal bones.

The Pachyosteina (Fig. 5G), the dominant placoderms of the Upper Devonian, are probably, though not certainly, a monophyletic group derived from the Coccosteidae. They are characterized particularly by a thoracic shield shortened dorsally and laterally, anterior laterals reduced ventrally to slender bones (Fig. 5G, Al), reduced or lost spinals, and pectoral fenestrae opened behind so that the bases of the pectoral fins could be lengthened. These trends were initiated in their coccosteid ancestors and are paralleled in some specialized families of Coccosteina. They differ from Coccosteina in having the posterior margin of the skull roof embayed, in the wider nuchal gap between the cranial and thoracic shields (Fig. 5G, ng), in the shorter nuchal plate with a pointed or rounded anterior margin and a concave posterior margin, and generally in the absence of prominent lobes on the central plates. They also show a tendency to lose tuberculation on the dermal bones.

Many Pachyosteina retain primitive, coccosteid-like characters among which are small orbits, long, loosely attached cheeks, a small nuchal gap, a relatively long median dorsal, rudimentary spinal plates, and tuberculated dermal bones. Another primitive character is an anteroventrally sloping neck-slit between the head and thoracic shield. This sloping neck-slit is retained by the Selenosteidae (Fig. 5G) which indicates that they were an early side-branch of the suborder, even though they do not appear until the Upper Frasnian. In many other respects the family was highly specialized, especially in the weak jaws, and in the orbits which had enlarged so much that the marginal plates formed their posterior boundaries and the cheeks were greatly shortened.

The Bungartiidae (new family), known only from a single Upper Famennian genus, *Bungartius,* is another family that retains the sloping neck-slit, but is peculiarly specialized in other ways. The preorbital part of the skull is greatly elongate, the nuchal gap is much enlarged due to the posterior projection of the paranuchal plates, and the jaws are shearing.

The Mylostomatidae are among the most specialized of Arthrodira with their durophagous jaws and their short, broad, flat shield. Their origin is obscure; they show some resemblances to Selenosteidae, but if *Tafilalichthys* is correctly referred here, it is possible that they were independently derived from primitive Pachyosteina.

Three families of Pachyosteina are distinguished by having the cheeks and gill covers extended posteriorly, resulting in a nearly vertical neck-slit. This may also give rise to a sharp angulation in the anterior lateral plates where they bend around and under the posterior edges of the gill covers. The first to appear, and in fact the earliest Pachyosteina, are the Dinichthyidae, which are mostly very large, broad-skulled forms with powerful, trenchant jaws bearing strong anterior cusps on the anterior supragnathals and infragnathals. The Leiosteidae are smaller forms with narrower skulls that are deeply embayed behind, and with crushing jaws. The third family, the Trematosteidae, has rather large orbits, long preorbital and short central plates, a postpineal fenestra, strong shearing jaws, and a tendency to deepen the cheeks and lower the jaw articulations. They are possibly related to Leiosteidae, but could not have been derived from known genera.

The last family referred to the Pachyosteina is the Titanichthyidae, which were highly specialized giants known only from the Famennian. Their shield is broad and depressed, and their jaws are long and slender, without teeth, cusps or shearing edges. Their origin is obscure but possibly lies in the primitive Dinichthyidae.

The two remaining suborders of Arthrodira include forms that have generally been referred to Brachythoraci or Pachyosteomorphi. The Heterostiina, including the single family Heterostiidae (Fig. 5I-J), would at first sight appear to belong to Pachyosteina. Like the Homostiidae and Titanichthyidae, it includes large forms with a broad, depressed head and body, but is distinguished by a characteristic posterior widening of the cranial roof. The latest forms have a very short thoracic shield (Fig. 5J) in which the anterior laterals send a long, tusklike process to meet the ventral shield, the latter a single plate lying far anterior under the head. Since the Heterostiidae occur in the Middle Devonian, it is not surprising to find that they retain a number of primitive characters. Among these are a relatively unspecialized cranial roof, a small nuchal gap, small anteriorly placed orbits that face anterolaterally (Fig. 5I, or), suborbital plates with short suborbital processes and long blades, and tuberculated dermal bones. However, in spite of their early appearance, they show no coccosteid characters and this, together with their phlyctaeniid orbits and suborbital plates, suggests for them a precoccosteid origin. If this is true, they are parallel to Pachyosteina, and thus referable to their own suborder.

The last suborder, the Brachydeirina (Fig. 5H), includes four genera grouped in two families, the Leptosteidae and Brachydeiridae, though the three genera of the second family are so distinctively specialized that each is commonly placed in a family of its own. In contrast to all other Arthrodira, the head and body are laterally compressed, high and elongate. In contrast to Pachyosteina, the lateral walls of the thoracic shield are not greatly reduced and large posterior laterals and posterior dorsolaterals are retained (Fig. 5H, Pl, Pdl). In spite of the long thoracic shield, deep pectoral emarginations (Fig. 5H, pe) separate the lateral and ventral shields except anteriorly, indicating probably that the pectoral fins were long-based. The nuchal gap is never enlarged and in one genus, *Synauchenia,* the cranial and thoracic shields have become sutured together, eliminating the neck joint completely. The Leptosteidae (Fig. 5H) have smaller orbits bounded posteriorly by postorbitals and suborbitals, and a very long, slender thoracic shield. The Brachydeiridae have larger orbits bounded posteriorly by marginals, and a shorter thoracic shield in which the ventral part may be reduced. The long thoracic shield of Brachydeirina indicates a derivation from a very primitive Coccosteina or perhaps even from one of the Phlyctaeniidae.

The last order, the Antiarcha (Fig. 5K), includes probably the most highly specialized of Placodermi. The thoracic shield is greatly elongated and has incorporated a second median dorsal plate (Fig. 5K, Pmd) behind the anterior one. Instead of pectoral fins, they have peculiar, usually jointed appendages, covered with small dermal plates (Fig. 5K, pa). Though often considered to be modified fins, these appendages were more probably derived from arthrodiran spinal plates. Their skulls, with their dorsal eyes and nostrils and large anterior premedian plate, are so modified that it is difficult to compare them with those of Arthrodira. Although antiarchs have been reported in China from beds that are supposed to be Lower Devonian, their first certain record is Eifelian. The first to appear are typical members of the order and so there are no intermediate forms to relate them to more typical placoderms. The elongate thoracic shield suggests an origin from primitive Arthrodira, and since their exoskeletal craniothoracic joint was certainly independently acquired, their ancestors probably are to be sought among Actinolepidae.

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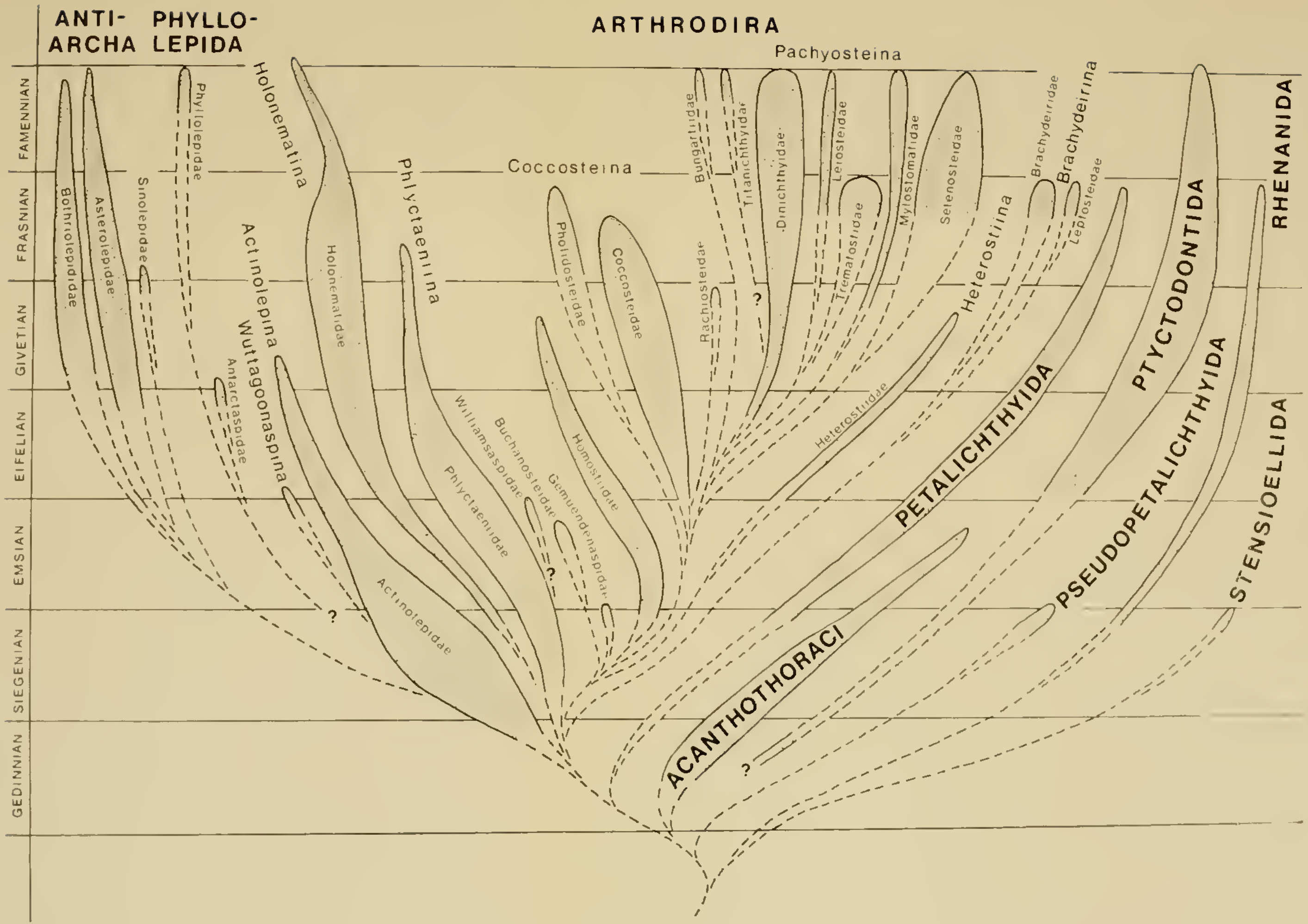
APPENDIX — CLASSIFICATION OF PLACODERMI

Class Pisces

Subclass Placodermi

Order Stensioellida	Family Stensioellidae
Order Rhenanida	Family Asterosteidae
Order Pseudopetalichthyida	Family Paraplesiobatidae
Order Ptyctodontida	Family Ptyctodontidae
Order Acanthothoraci	Family Palaeacanthaspidae
	Family Radotinidae
	Family Kolymaspidae
Order Petalichthyida	Family Macropetalichthyidae
Order Arthrodira	
Suborder Actinolepina nov	Family Actinolepidae
Suborder Wuttagoonaspina	Family Wuttagoonaspidae
Suborder Phlyctaeniina	Family Phlyctaeniidae
	Family Williamsaspidae
Suborder Holonematina	Family Holonematidae (including Groenlandaspididae)
Suborder Coccosteina	Family Gemuendenaspidae
	Family Buchanosteidae
	Family Coccosteidae
	Family Pholidosteidae
	Family Homostiidae (including Euleptaspidae)
	Family Rachiosteidae
Suborder Pachyosteina	Family Dinichthyidae
	Family Titanichthyidae
	Family Leiosteidae
	Family Trematosteidae
	Family Mylostomatidae
	Family Selenosteidae
	Family Bungartiidae nov.
Suborder Heterostiina	Family Heterostiidae
Suborder Brachydeirina nov.	Family Brachydeiridae
	Family Leptosteidae
Order Phyllolepida	
Suborder Antarctaspina	Family Antarctaspidae
Suborder Phyllolepina	Family Phyllolepidae
Order Antiarcha	Family Bothriolepididae
	Family Asterolepidae
	Family Sinolepidae

Figure 6. Phylogenetic chart of Placodermi. Each branch represents a family except in Acanthothoraci which includes three families. The width of the branches is determined by the number of genera. →


ANTIARCHA
PHYLLOLEPIDA
ARTHRODIRA
Pachyosteina
Coccosteina
FAMENNIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
SIEGENIAN
GEDINNIAN
Bothriolepididae
Asterolepidae
Sinolepidae
Phyllolepidae
Antarctaspidae
Actinolepina
Wuttagoonaspina
Holonematina
Holonematidae
Actinolepidae
Phlyctaeniina
Phlyctaeniidae
Williamsaspidae
Buchanosteidae
Gemuendenaspidae
Homostiidae
Pholidosteidae
Coccosteidae
Bungartiidae
Titanichthyidae
Dinichthyidae
Rachiosteidae
Leiosteidae
Trematosteidae
Mylostomatidae
Selenosteidae
Heterostiina
Heterostiidae
Brachydeiridae
Brachydeirina
Leptosteidae
PETALICHTHYIDA
PTYCTODONTIDA
PSEUDOPETALICHTHYIDA
RHENANIDA
STENSIOELLIDA
ACANTHOTHORACI
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SOUTH AMERICAN *ANOLIS*: *ANOLIS IBAGUE*, NEW SPECIES OF THE *PENTAPRION* GROUP FROM COLOMBIA

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Abstract. *Anolis ibague,* new species, is described on the basis of a single juvenile female. It is regarded as a distinctive peripheral member of the *Anolis pentaprion* group.

In a series of *Anolis antonii* received from the Vienna Museum is a single small female anole with quite distinctive head and dorsal scalation. It is clearly new and I name it after the locality at which it was collected:

Anolis ibague, new species

Holotype: Vienna 18942:38; a juvenile female.
Type locality: Ibague, Dto Tolima, Colombia.

Head. Head scales smooth, imbricate, those in frontal depression larger than any on the snout. Scales across snout between second canthals 8. 8 scales border rostral posteriorly. Anterior *and* inferior nasal scales in contact with rostral. Six swollen but narrow scales between supranasals.

Scales of supraorbital semicircles very broadly in contact, all very large, the second and third pair relatively larger, the third pair in contact with the enormous interparietal. Scales of supraocular disk about 16 in number, smooth, in contact with supraorbital semicircles. Supraciliaries elongate, single, followed by granular scales. Six canthal scales, canthus falling well short of nostril, separated by swollen subgranular scales. Five loreal rows, uppermost and lowermost largest. Temporal and supratemporal scales subgranular, not swollen. No differentiated supratemporal line. Supratemporal scales gradually enlarging toward the interparietal, with the scales immediately lateral and anterolateral to the interparietal very large. One row of large scales posterior to the interparietal immediately followed by scales similar to those of the back.

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Suboculars in contact with supralabials. 6–7 supralabials to the center of the eye.

Mental wider than long, in contact with only two small scales between the very large sublabials. Four sublabials on each side in contact with the infralabials.

Throat and anterior chin scales between the sublabials laterally large, becoming smaller centrally and posteriorly.

Trunk. Middorsal scales slightly larger than the lateral granules. Lateral granules becoming larger, merging into the much larger smooth and imbricate ventrals.

Dewlap (juv. ♀). Absent. The merest indication in a very small central fold, the scales *not* enlarged.

Limbs and digits. Scales of upper arm, front of thigh and lower leg smooth. Those of lower arm unicarinate. Those of digits weakly multicarinate. 19 lamellae under phalanges ii and iii of 4th toe.

Tail. Compressed. No enlarged postanals. No tail crest, a double line of weakly keeled scales middorsally. Most ventral tail scales more distinctly keeled but scales immediately behind vent smooth.

Color. A white middorsal zone diminishing to a point on the occiput but continuing on tail. Head dark, vaguely marked with lighter. Flanks light purplish, spotted and flecked with darker purple. Belly and throat lighter, the throat spotted, the belly more indistinctly tinged with darker.

COMPARISONS

The affinities of *Anolis ibague* would appear to lie with those beta anoles with smooth ventrals, suboculars in contact with supralabials and counts of fourth toe lamellae between 15 and 20.

On the one hand this would appear to ally *ibague* with the fuscoauratus complex, and it is in fact sympatric, perhaps syntopic, with one member of this series— *antonii*. Not surprisingly, *A. ibague* more closely resembles a species not sympatric with it, *A. ortoni,* a species widely distributed throughout Amazonia. *A. ortoni* approaches *A. ibague* in its large interparietal and its supraorbital semicircles in contact. It differs in having small scales, like those of the dorsum, behind the interparietal. *A. ortoni* resembles *A. ibague* in the presence of a middorsal light stripe in the female. (This, however, is a character frequently present in female anoles, even in very distantly related species.) It differs in a tendency to a higher number of loreal rows and in having the scales immediately behind the interparietal small like the dorsals. Neither the resemblances nor the differences are unique or special.

There appear to be greater resemblances to the *pentaprion* group which has now been described in some detail by C. W. Myers (1971) with the description of two new species and the restoration from synonymy of a third.

Myers has defined the *pentaprion* group in the following terms: "Beta anoles of small to moderately large size, relatively short legs (appressed hind limbs usually failing to reach ear, never reaching eye); digital pads dilated, with distal phalanx raised from the dilated pad; low loreal region (maximum of 2–5 horizontal scale rows); black throat lining and parietal peritoneum; a bluish gray or blue-covered sliver of tissue at the corner of the mouth; few rows of scales on dewlap of relatively persistent (i.e. fade resistant in preservative) red or purple coloration; tendency for lichenose or fungous color pattern (in two of three species); no vertebral stripe; tendency for smooth scales over most of the head and body; relatively small dorsal and ventral trunk granules; ventral granules tending to obliquely conical (ontogenetic change to flat and imbricate in one species)."

Some of these characters cannot be determined in the unique preserved type, and others do not apply. However, Myers has already been forced to acknowledge occasional exceptions to his character list, and some characters such as the absence of a vertebral stripe in the female are the sort of characters that are provisionally accepted as part of a group definition in a small sample of species but are discarded without hesitation if the ensemble of characters proves that a species belongs in a group. The light vertebral streak has apparently been evolved many times within the genus *Anolis,* and its appearance in yet another species, whatever its relationships, causes no surprise.

I would place especial reliance on some of Myers' characters and add certain others. Thus, smooth scales on head and body are at one end of a spectrum that in the genus as a whole varies from completely smooth to rugose and heavily keeled. In any small set of closely related species, smooth scales are likely to be consistent. Similarly likely to be good group characters are low loreal counts (lower than 6) and short limbs.

Quite as useful — ordinarily — are contact between suboculars and supralabials and low counts across the snout between posterior canthals (<10). In some species there is considerable variability in these regards; more often these two conditions are reliable group characters.

In these features in which I would place considerable confidence — they are more distinctive within the beta section of *Anolis* than in alphas — *A. ibague* fits the *pentaprion* group.

DISCUSSION

The single individual described above seems to be a *juvenile* female. As such it will not appear to be the best material on which to base a new taxon. Barbour (1934) has commented: "It is most unfortunate to describe *Anolis* from single female specimens as also Boulenger did on all too many occasions."

Barbour's philosophy, widely shared, rests upon the general proposition that male *Anolis* are often more distinctive in both scale and color characters than females of their species. This is undoubtedly true. Underwood and Williams (1959), speaking of Jamaican anoles, said: "The males of the various forms are far more clearly differentiated than the females. The possession of a fan by the male contributes to this, but the color of pattern of the males is always more distinctive. In some cases females are almost impossible to distinguish . . . Descriptions of species founded only on female material are of limited value."

Again the truth of this for Jamaican animals would be difficult to deny, but they represent a small radiation that, despite significant differences in ecology and size, is still remarkably close knit. In similar mini-radiations of anoles it is often true that the color patterns and the spectacular dewlaps of males may be, like the voices of male frogs, the major way in which the species tell themselves apart.

However, in this, as in so many cases, no rigid rules apply. The variability of each group and subgroup is peculiar to itself alone and must be empirically determined. Males are in anoles the sex of choice for species descriptions, but sex dimorphism in anoles does not go so far that valid species *cannot* be recognized on females alone. Sexual dimorphism in *Anolis* is most often evident in color and size, much more rarely in the general characters of scalation. Aspects of morphology most probably associated with social interaction and display — dewlaps, the probosci of proboscis anoles, tail crests, etc. — are apt to be sexually dimorphic. Sometimes there may be differences in head scales but these are minor, e.g., greater keeling of all head scales in females than in males, as in *females* of the *Anolis homolechis* series of Cuba. In no case are scale differences of the kind that would permit belief that male and female are quite distinct species; at most they are differences of the kind that could be expected to occur between males of very closely related, doubtfully distinct species.

Color differences are often more radical, but here in anoles sharp differences may occur as morphs within well-understood species or even, not at all unusually, between phases in the same individual.

In any case, the problem of *Anolis ibague* is not that it is rather characterless or differs only in subtleties from any other anole. On the contrary, its characters are extreme for its group and relatively extreme within anoles.

The characters of *A. ibague* that are extreme are the great size of the interparietal, of certain of the supraorbital scales, and of the sublabials.

The size of these scales in the *juvenile* type specimen may well be more extreme than in adults of the species. Some head scales are often relatively larger in very young specimens of any species. But, although the enlargement of certain head scales is greater in *ibague* than in any related species, and these scales are at one end of the curve of head scale variation for the genus *Anolis* as a whole, they are, however, nearer the taxonomic norm for such iguanid genera as sceloporines or tropidurines, for which a huge interparietal and large supraorbital scales are in fact partly diagnostic. There is nothing anomalous about these conditions: they are merely highly derived character states.

The discussion of relationship above has suggested that *ibague* is a local representative in central Colombia of a group — the *pentaprion* group — otherwise unknown there. Special peculiarity in a peripheral isolate is not unusual; it seems the preferable explanation of the exceptional features of this species.

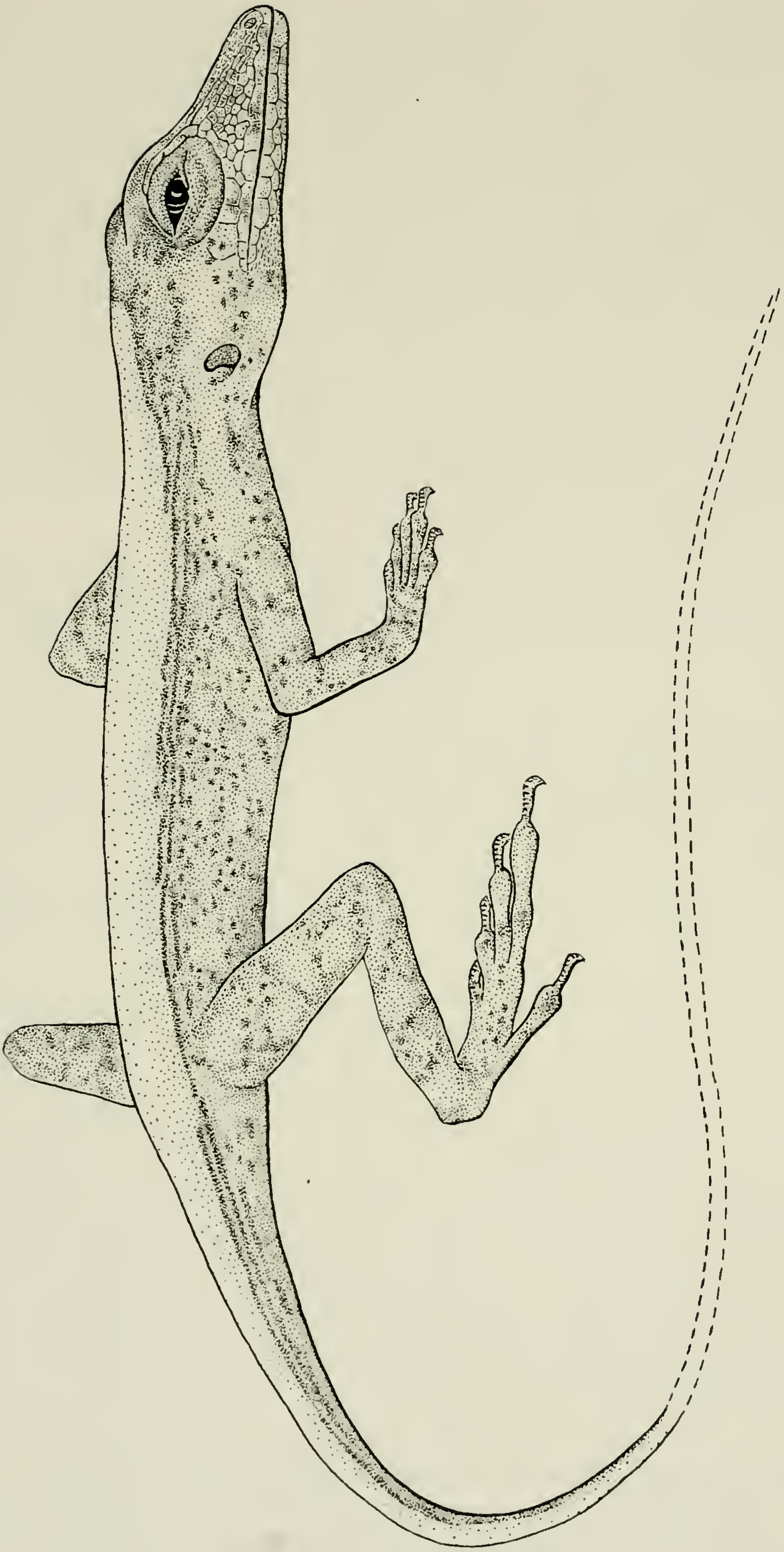

Fig. 1. *Anolis ibague* Type. Lateral view to show pattern.

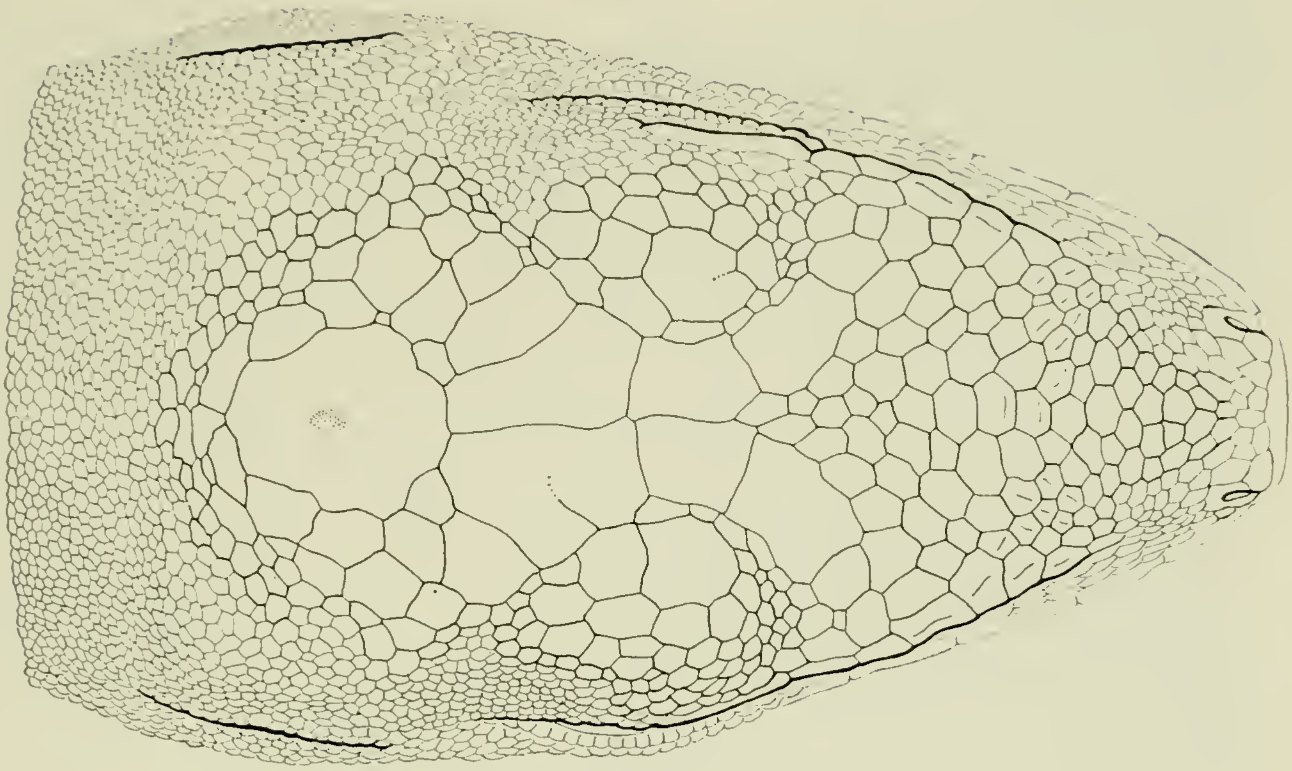

Fig. 2. *Anolis ibague* Type. Dorsal view of head scales.

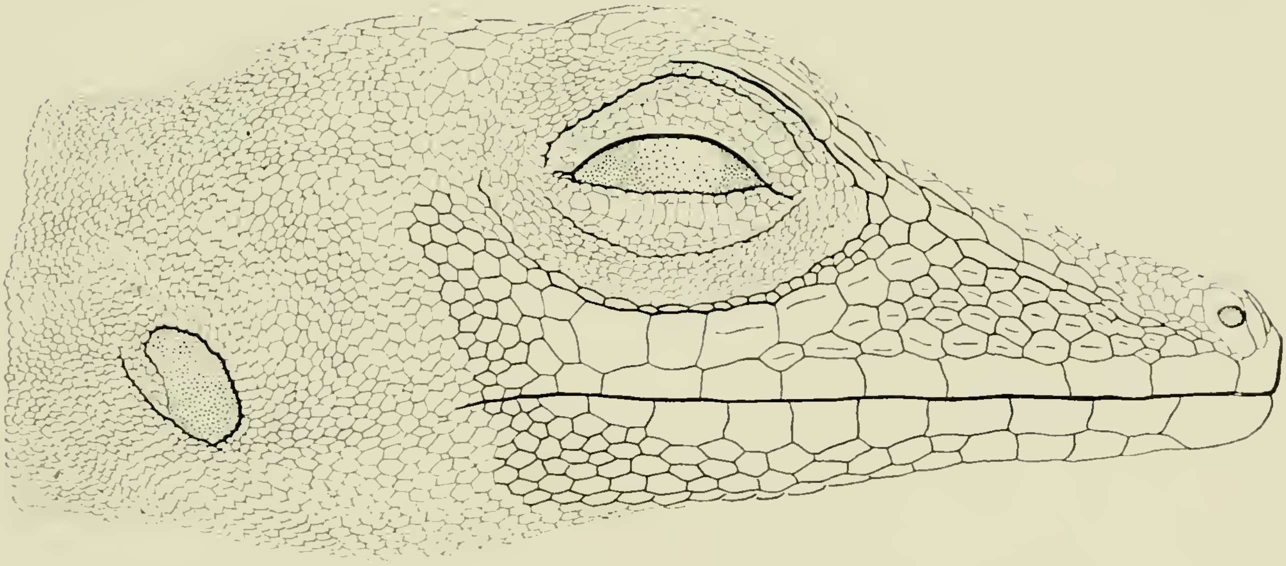

Fig. 3. *Anolis ibague* Type. Lateral view of head scales.

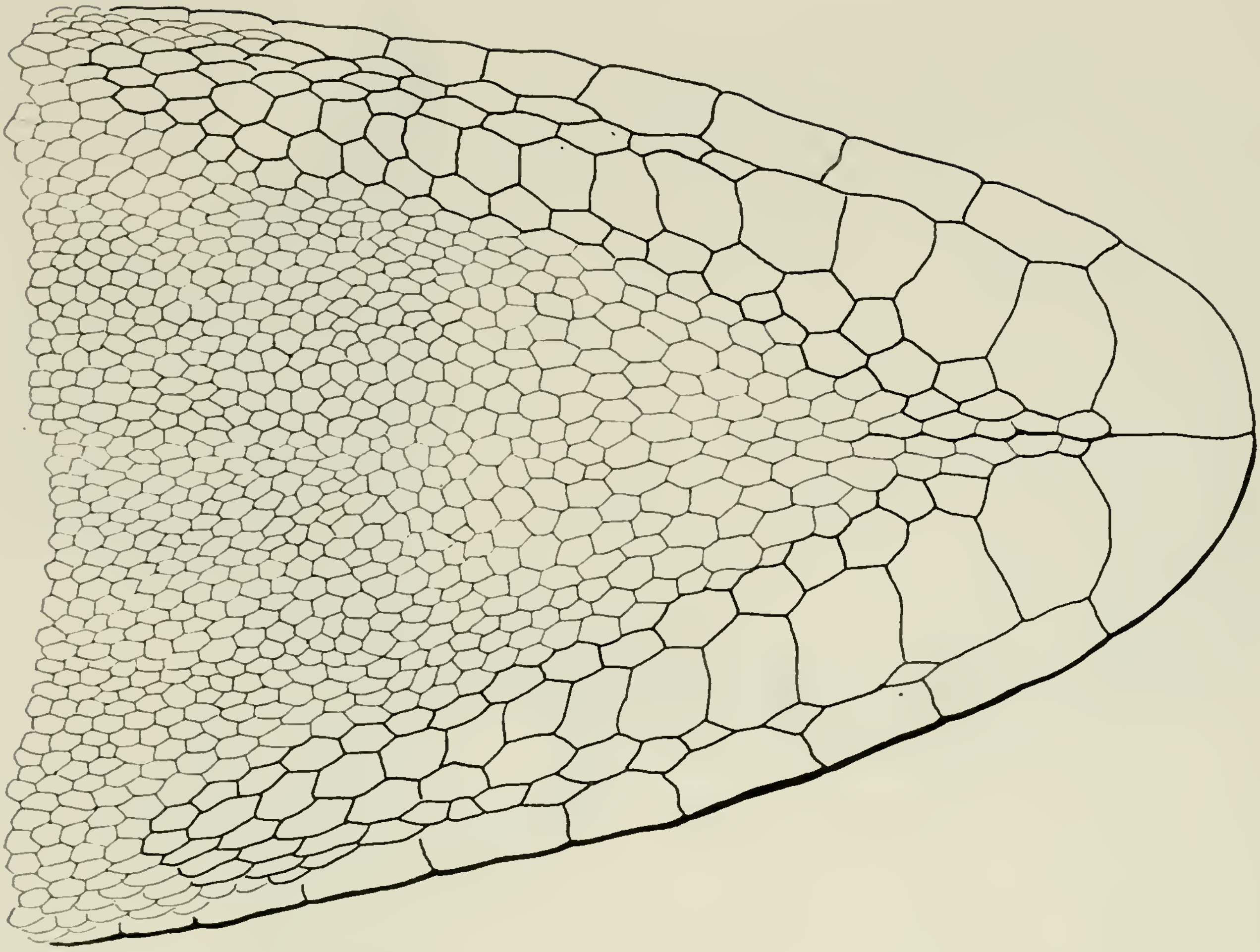

Fig. 4. *Anolis ibague* Type. Ventral view of chin scales.

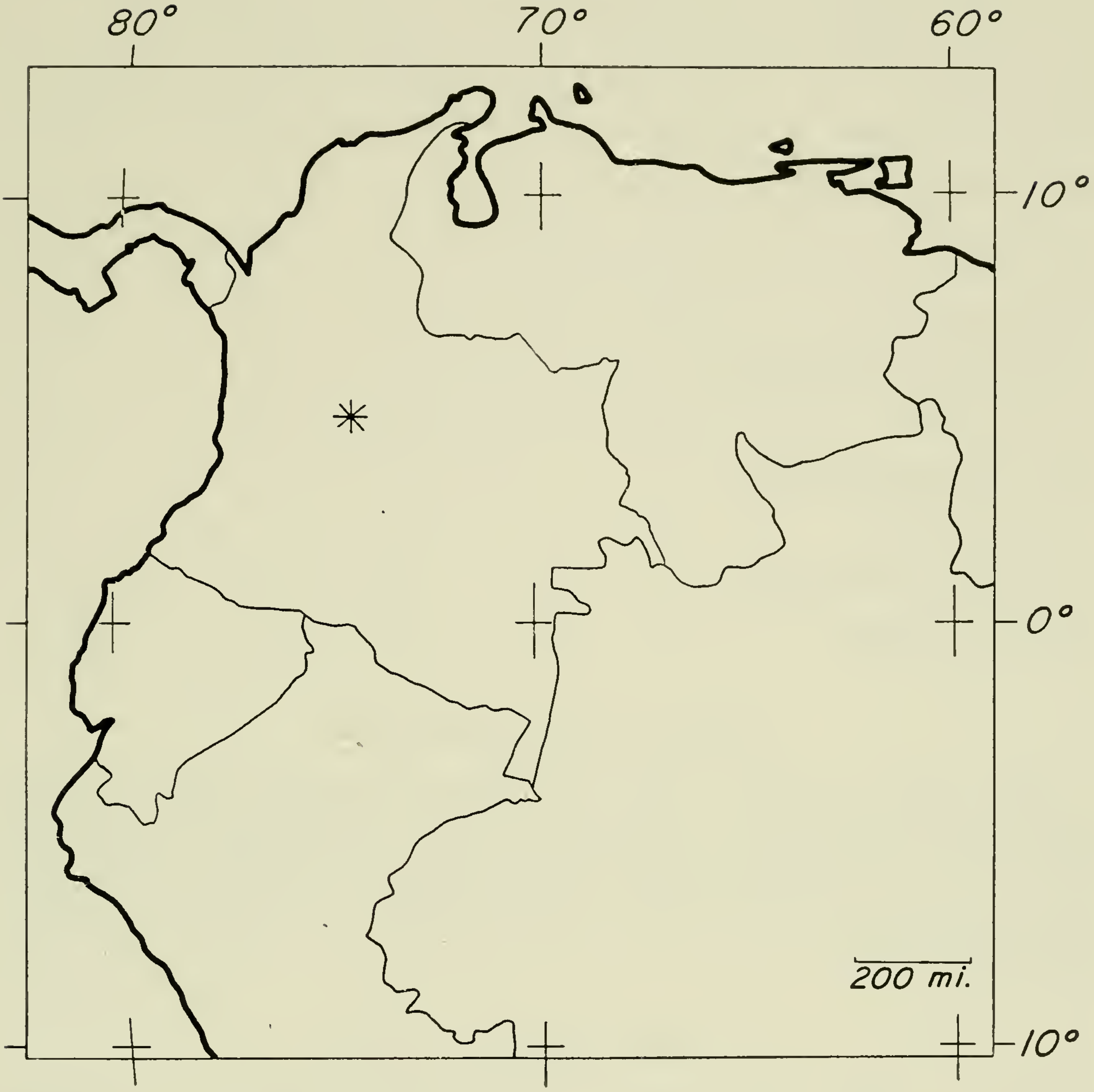
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Fig. 5. Asterisk indicates type locality of *A. ibague*.

Table 1. Scale characters of *A. ibague* compared.

	ibague	*sulcifrons*	*fungosus*	*vociferans*	*pentaprion*
scales across snout	10	8	7	7–13	7–14
scales between semicircles	0	0	1–2	0–2	0–2
loreal rows	5	5	3	3–5	2–5
interparietal/ear	>	>	>	>	>
scales between interparietal and semicircles	0	1	1–3	2	1–3
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	6	6	7–8	6–8	7–10
fourth toe lamellae	17	18	17	18	19–24

ACKNOWLEDGMENTS

The study of South American anoles of which this is a part has been supported by National Science Foundation Grant GB 37731X and previous grants. Dr. Joseph Eiselt of the Vienna Museum generously loaned the material in which *A. ibague* was discovered.

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CAMBRIDGE, MASS. 19 SEPTEMBER 1975 NUMBER 434

SOUTH AMERICAN *ANOLIS*: *ANOLIS PARILIS*, NEW SPECIES, NEAR *A. MIRUS* WILLIAMS

ERNEST E. WILLIAMS[1]

ABSTRACT. *Anolis parilis* is described as the west Ecuadorian representative of *A. mirus* from the Rio San Juan, Colombia. *A. parilis* differs from *A. mirus* in a number of ways, all individually minor, but sufficient in sum to indicate species status.

The species *Anolis mirus* was described (Williams, 1963) from a single specimen with the imprecise locality "Rio San Juan Colombia." No further specimens have been collected in the intervening years.

However, another single specimen, obviously related, has come to hand from intermediate elevations in Ecuador. Despite its closeness to *A. mirus*, even in characters quite special to that species, it appears to differ enough to deserve description as a new species which I name because of its similarity as:

Anolis parilis n. sp.

Type. UIMNH 82901, an apparently adult male.

Type locality. Rio Baba, 2.4 km S Sto Domingo de los Colorados, Pichincha, Ecuador. George Key, collector. November, 1965.

Diagnosis. Very close to *A. mirus* but differing in color, in smooth rather than keeled ventrals and in other minor scale characters. Perhaps also different in size.

Head. Head scales small, weakly keeled. About 17 scales across snout at level of second canthals. Six scales bordering rostral posteriorly. Anterior nasal separated from rostral by one scale. Seven scales between supranasals.

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At least 4 scales between supraorbital semicircles, the scales of which are not much enlarged. Supraocular disk not differentiated. A short supraciliary on each side followed by granules. Canthus distinct, 9 canthal scales, the fourth largest. Seven loreal rows below third canthal (2nd canthal *behind* level of loreal rows on the rise of the orbit). Uppermost and lowermost loreal rows largest.

Temporal and supratemporal scales granular. An indistinct double line of enlarged granules at margin between supratemporal and temporal areas. Scales around interparietal larger. Interparietal about equal to ear opening, separated from supraorbital semicircles by six scales.

Suboculars narrowly in contact with supralabials, posteriorly grading into upper temporal granules, anteriorly separated by one scale from canthal ridge. Nine supralabials to below center of eye.

Mentals wider than deep, in contact with eight scales between infralabials. No differentiated sublabials. Central throat scales smallest, grading laterally into larger distinctly keeled scales.

Trunk. Two middorsal rows tending, especially on nape, to be conical, enlarged, smooth, subimbricate. Ventrals larger than dorsals, subquadrate, smooth.

Dewlap. Large, extending onto first third of belly. Edge scales about equal to ventrals. Lateral scales much smaller than ventrals, in rows, widely separated by naked skin. Above dewlap on sides of neck complex folding between ear and shoulder.

Limbs and digits. Largest arm and leg scales about equal to ventrals and weakly unicarinate except those of elbows and knee larger and multicarinate. Supradigital scales multicarinate. Fifteen scales under phalanges ii and iii of fourth toe; distal phalanx not raised.

Tail. Compressed, without crest. Dorsalmost scale row single, keeled. Ventralmost scales larger, strongly keeled. Postanals irregularly enlarged.

Color (as preserved). Red-brown with a narrow black middorsal line. Black mottling tending to transverse banding on side of neck and lower flanks.

Size. 81 mm, snout-vent length.

Discussion. The resemblances and differences between *A. parilis* and *A. mirus* are made clear in Table 1. The differences are just sufficient to imply species distinction given that there are only two specimens before us. Size appears to differ but it is precisely in the larger species of *Anolis* that there is a long period of growth after sexual maturity. The color and pattern of the two are radically different as preserved, but neither are known from life. It is improbable but not impossible in a genus such as *Anolis* that a difference as great as seen here could exist in the color repertoire of a single species. No single one of the scale differences — smooth versus keeled ventrals, suboculars in contact with supralabials rather than separated by one scale row, the greater number of scales across the snout, the different rostral-nasal relationship, etc. — are quite outside the possibility of intraspecific variation. Taken together, however, they point to a high probability of specific difference, i.e., genetic discontinuity.

Nothing is known of the ecology of either of these species. The few suggestions that can be made are inferences from structure only. The narrow toe pads without a raised anterior margin (the condition described as the diagnostic character of the invalid genus *Norops*) are characteristic of some anoles that are not arboreal but are grass or ground dwellers; this is a derived condition within anoles that has been evolved repeatedly. Most *Norops*-like anoles are small (less than 60 mm snout-vent length), but the South American group to which *parilis* and *mirus* seem to belong — the *eulaemus* species group — verges on giant size (arbitrarily defined for *Anolis* as 100 mm snout-vent length). Within the *eulaemus* group two subgroups may be distinguished, one of which has the toe pads narrow but with a "raised" distal edge — the *eulaemus* group s. str. — and another with the toe pads *Norops*-like. The latter is the subgroup to which *parilis* and *mirus* belong along with *A. aequatorialis* (the ecology of which again is quite unknown). A combination of giant size and toe pads that are poorly differentiated would suggest a ground dweller. The artist who drew *mirus* in fact showed the animal on a rocky substrate — on no evidence whatever (Fig. 2, Williams, 1963). In fact, however, both *parilis* and *mirus* have the first phalanx of each digit enlarged and strengthened (shown well in *mirus* in Fig. 1, Williams, 1963), a fact that probably does imply climbing propensities but with claws not pads. No more can be said until observations on the live animals are reported.

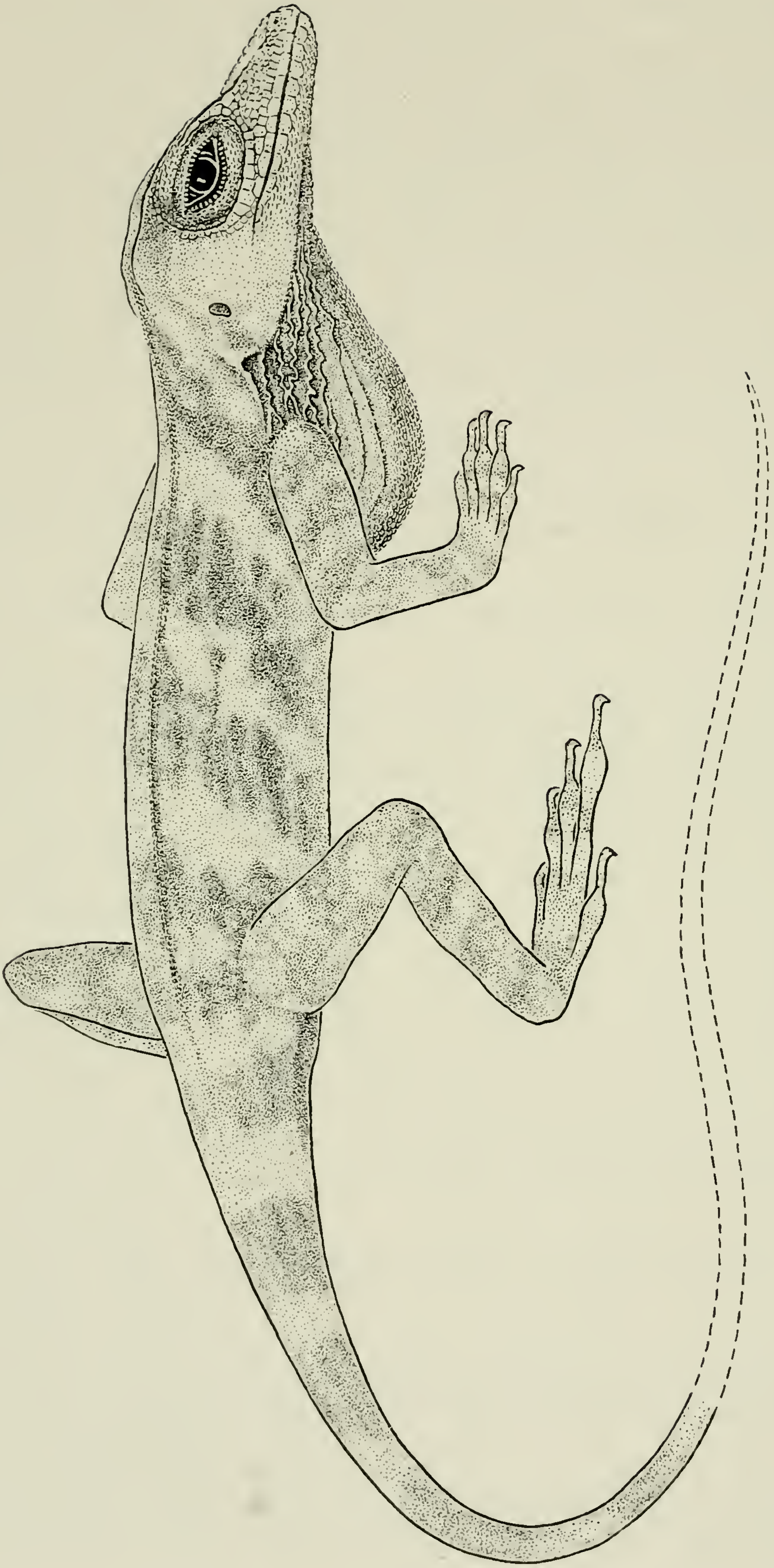

Fig. 1. *Anolis parilis* Type. Lateral view to show pattern.

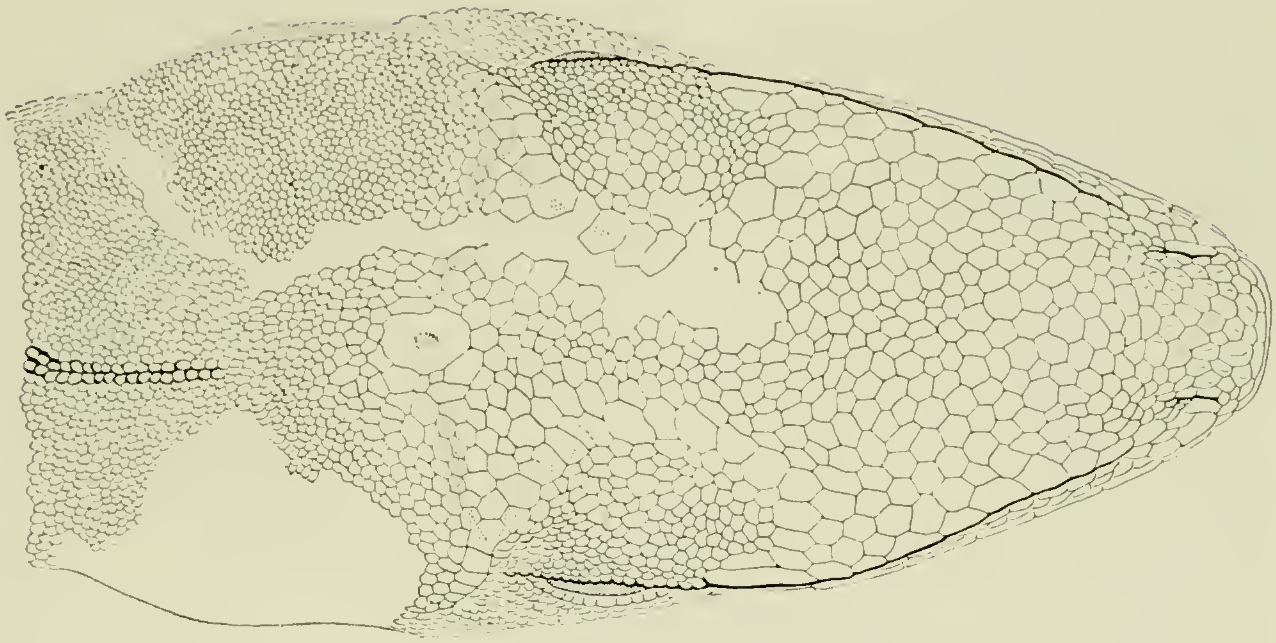

Fig. 2. *A. parilis* Type. Dorsal view of head scales.

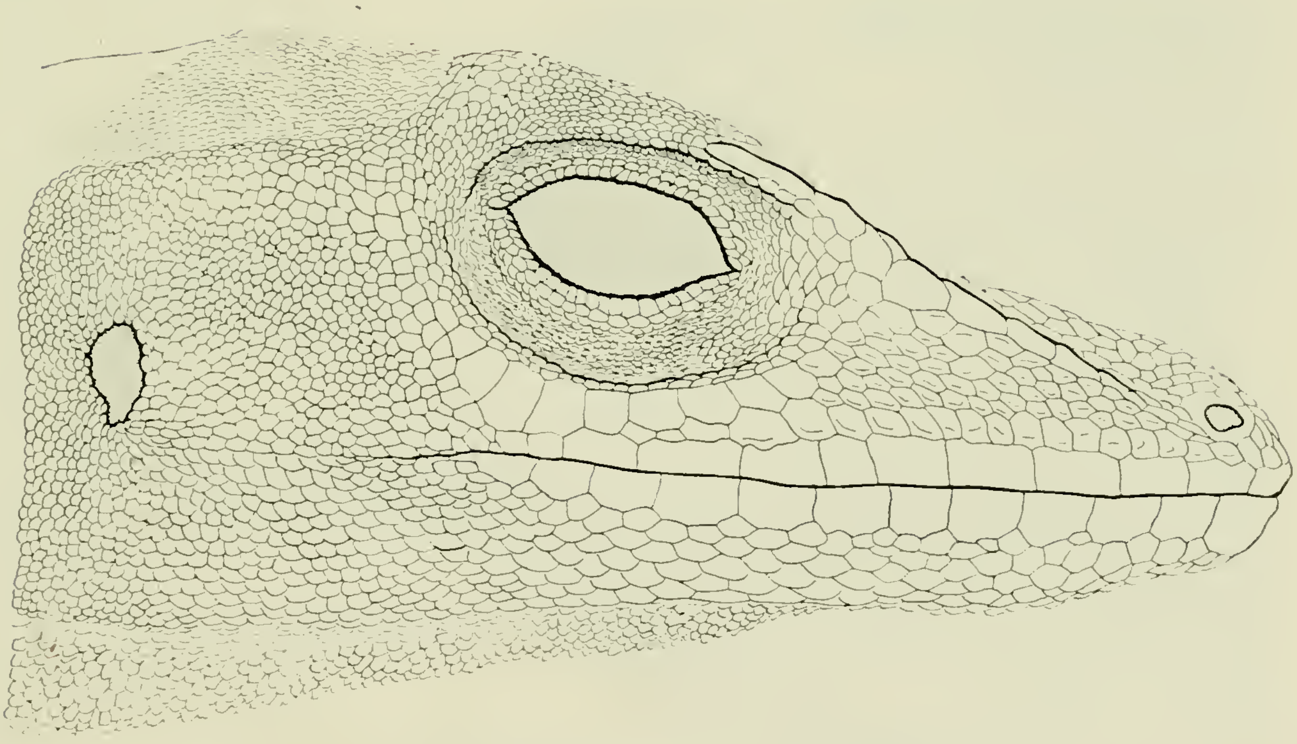

Fig. 3. *A. parilis* Type. Lateral view of head scales.

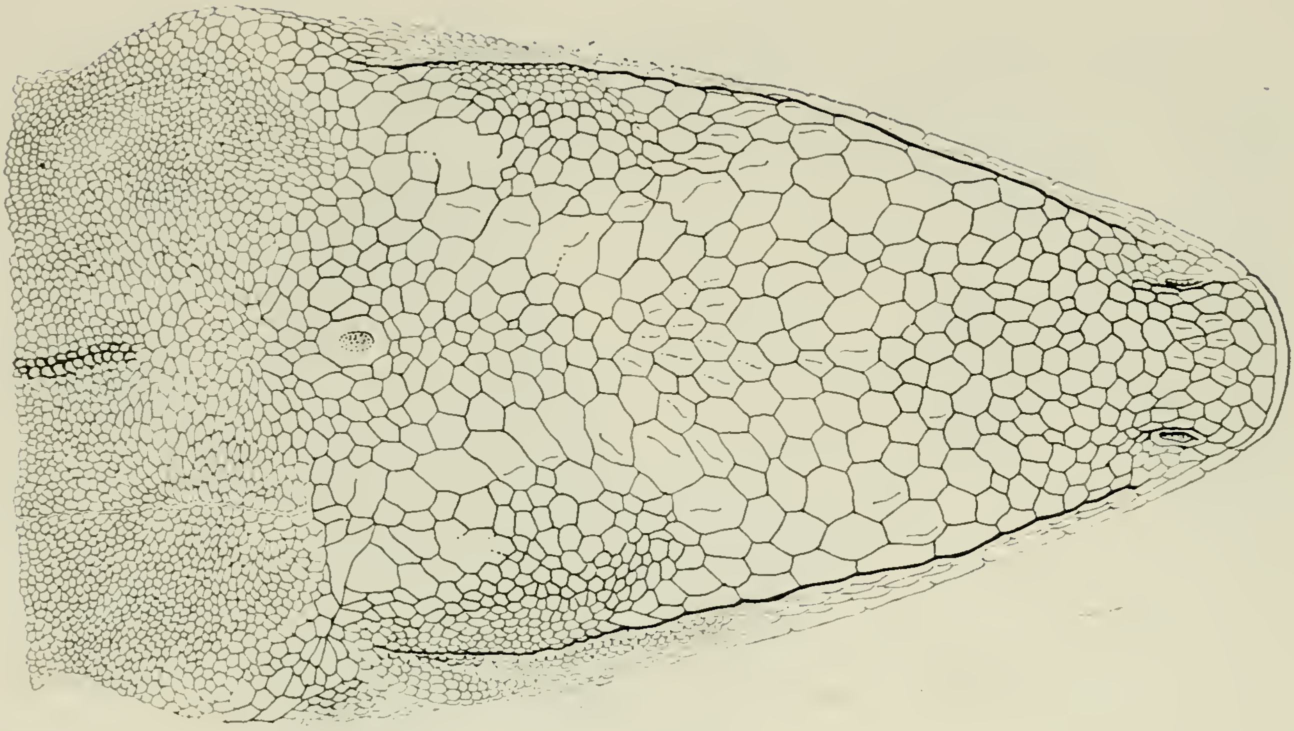

Fig. 4. *A. mirus* Type. Dorsal view of head scales.

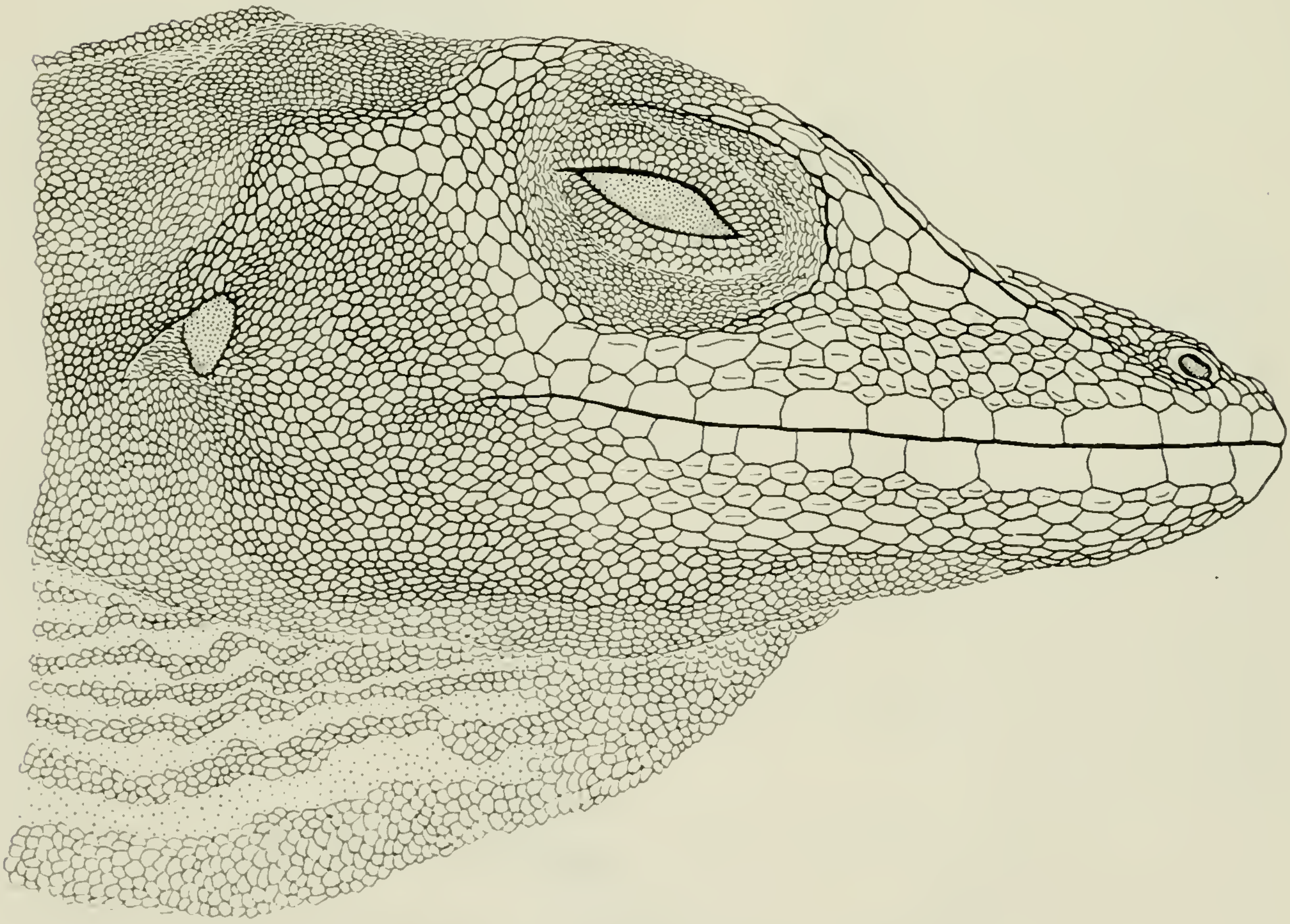

Fig. 5. *A. mirus* Type. Lateral view of head scales.

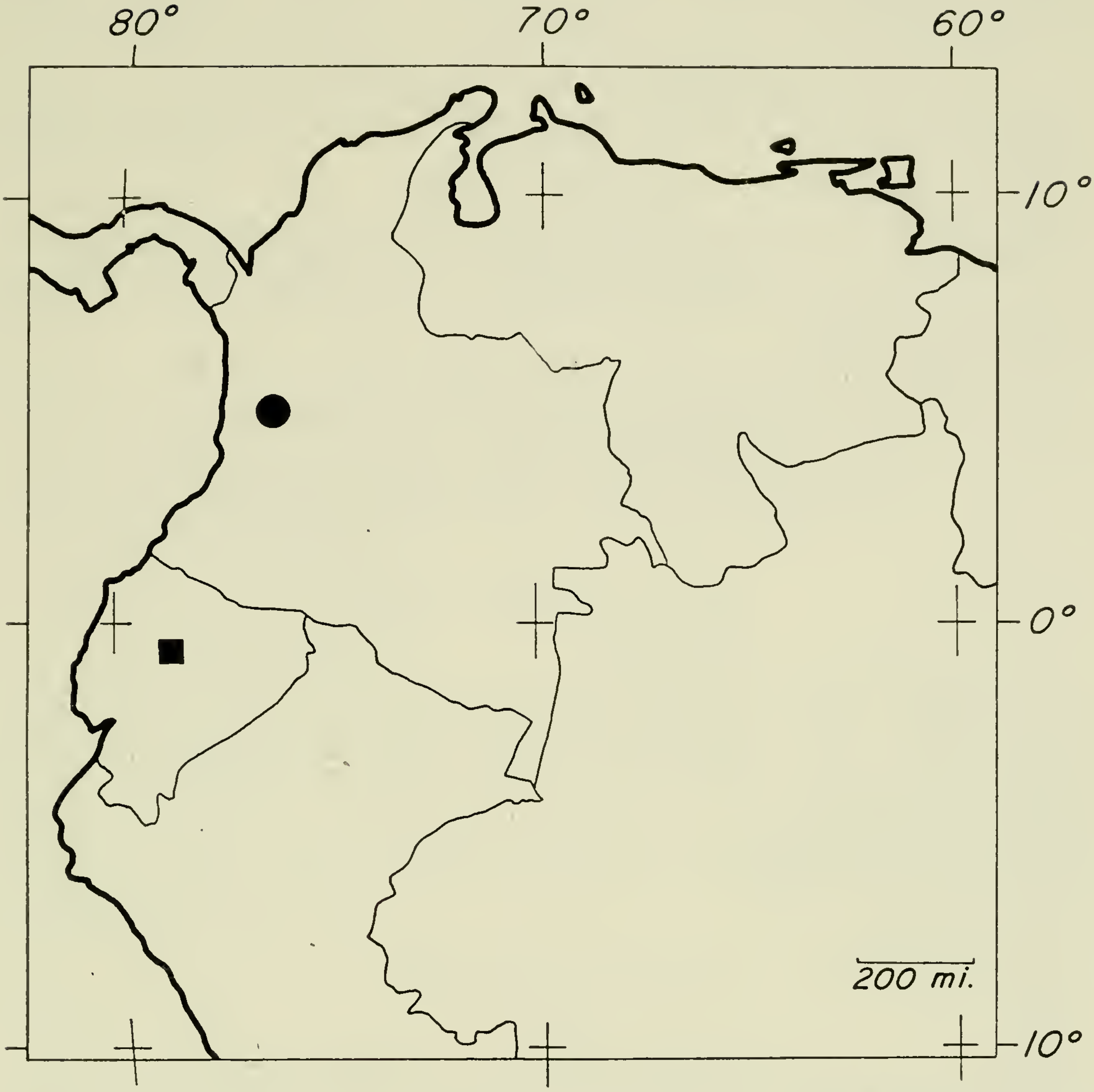

Fig. 6. Dark circle = type locality of *Anolis mirus.* Dark square = type locality of *Anolis parilis.*

ACKNOWLEDGMENTS

Description of *A. parilis* was made possible by the studies of South American anoles that continue under National Science Foundation Grant GB 37731X and previous grants. My thanks go also to the authorities at the University of Illinois who made the unique type available to me.

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Williams, E. E. 1963. Studies on South American anoles. Description of *Anolis mirus,* new species, from Rio San Juan, Colombia, with comment on digital dilation and dewlap as generic and specific characters in the anoles. Bull. Mus. Comp. Zool. **129:** 463–480.

TABLE 1

Comparison of *A. parilis* and *mirus.*

	parilis	*mirus*
scales across snout	17	12
rostral/nasal	*one* scale between nasal and rostral	*two* scales between nasal and rostral
scales between supraorbital semicircles	4	4
supraciliaries	one (short) followed by granules	on one side the same; on the other one (short) and granules in the middle of the supraciliary margin and enlarged scales posteriorly
temporal line	a very *indistinct* double line	a triangle of *distinctly* enlarged scales
scales around interparietal	*gradually* larger than dorsals or temporals	*abruptly* larger than dorsals or temporals
rows between interparietal and semicircles	6	4
rows between suboculars and supralabials	0	one *interrupted* row
supralabials to center of eye	9	10
mental	wider than deep	wider than deep
scales in contact with mental between infralabials	8	6
sublabials	not differentiated	same
dewlap	large, scales in *weakly defined* rows, edge scales ca = ventrals, complex folding between ear and shoulder	large, scales in *well defined* rows, edge scales ca = ventrals, complex folding between ear and shoulder
adhesive pad	not set off from first phalanx (*Norops* condition)	same
lamellae under phalanges ii and iii of fourth toe	15	15
snout-vent length	81 mm	116 mm

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TWO NEW SPECIES OF *CHELUS* (TESTUDINES: PLEURODIRA) FROM THE LATE TERTIARY OF NORTHERN SOUTH AMERICA

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Abstract: Two new species of the pleurodiran turtle *Chelus* are described from the late Tertiary of northern South America. These are the first valid extinct species of the genus to be described. Both occur outside the present range of the single living species, *C. fimbriatus,* and neither appears to have been directly ancestral to it. Observations on variability in a sample of *C. fimbriatus* shells are recorded to facilitate comparisons with the fossils.

INTRODUCTION

Of the world's living turtles, the most bizarre in appearance is unquestionably the mata-mata, *Chelus fimbriatus.* Its shell is gnarled and serrated, while its broad and extraordinarily flat head, festooned weirdly with fleshy tendrils, looks as if it were the product of some science fiction writer's fevered imagination. This species at present enjoys a widespread distribution throughout the Amazon and Orinoco River basins of tropical South America. Yet surprisingly little is known about the behavior, ecology, or intra- and interpopulational variation of this peculiar creature, and virtually nothing is known about its ancestry.

The purpose of this paper is to put on record two species of the genus from Tertiary sediments of northern South America. These are the first fossil remains of *Chelus* well enough preserved to permit determination of diagnostic characters, and knowledge of them provides the first, albeit imperfect, glimpse into the evolutionary history of the genus. One of these species, from the late Miocene of Colombia, was discovered during the mid-1940's by the late Dr. R. A. Stirton and his associates from the University of California Museum of Paleontology and the Geological Survey of Colombia. Occasional reference to the existence of this material has been made over the years (e.g., Royo y Gomez, 1945; Stirton, 1953; Medem, 1968), but until now it has not actually been described. Remains of the other new species, from beds of Huayquerian age in northern Venezuela, were collected during the summer of 1972 by the author and colleagues from Harvard's Museum of Comparative Zoology.

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The following abbreviations are used:

AMNH — American Museum of Natural History
BMNH — British Museum (Natural History)
GMB — Museum of the Geological Survey of Colombia, Bogotá
MCNC — Museo de Ciencias Naturales, Caracas
MCZ — Museum of Comparative Zoology, Harvard University
MZUSP — Museo do Zoologia, Universidade de São Paulo
PCHP — personal collection, Dr. P. C. H. Pritchard
UCMP — University of California Museum of Paleontology
USNM — United States National Museum of Natural History

CLASSIFICATION AND DESCRIPTION

Order Testudines
Suborder Pleurodira
Family Chelidae
Genus *Chelus*

Chelus colombianus sp. nov.

Plates 1–3, Figure 1

Type. UCMP 78762, a nearly complete shell.

Hypodigm. The type, and GMB 2045A, an incomplete shell lacking part of the right side of the carapace and the anterior plastral lobe; GMB 2049, a partial shell, completely disarticulated; GMB 2446, carapace fragments; GMB 2085, left epiplastron; GMB 2242, left hyoplastron; GMB 2042, GMB 2089, and UCMP 38851, neurals; and UCMP 38838, a peripheral; all from the vicinity of Villavieja.

GMB 1844, a left xiphiplastron; UCMP 39014 and UCMP 39024, neurals; all from the vicinity of Carmen de Apicalá.

GMB 1885 and GMB 1891, left xiphiplastra; GMB 1934, right hyoplastron; all from the vicinity of Coyaima.

GMB unnumbered, posterior left quadrant of a carapace, locality unknown.

Horizon and localities. Villavieja Formation (late Miocene), upper Magdalena River Valley, Colombia.

The specimens making up the hypodigm were collected in the vicinity of three settlements, Coyaima, Carmen de Apicalá, and Villavieja, the majority coming from the last (see above). Stirton (1953) designated the fossil vertebrates from these three different localities as, respectively, the Coyaima, Carmen de Apicalá, and La Venta faunas. The first of these he regarded as being of late Oligocene (Colhuehuapian) age while to the latter two he assigned a late Miocene date. Subsequently, Fields (1957) suggested that the Coyaima fauna was of the same age as the others. Bryan Patterson (personal communication) informs me that he tends to agree with Fields, being unable to see anything diagnostically Colhuehuapian in the published account of the scanty and fragmentary Coyaima mammalian faunule. As regards the hypodigm of the species here described, it is not possible to differentiate the few Coyaima fragments from the remainder.

The strata containing these fossils all belong to the Honda Group. These rocks have recently been subdivided into two formations, the lower termed the La Dorada and the upper the Villavieja (Wellman, 1970). The vertebrate-bearing sediments are apparently confined to the Villavieja Formation (Van Houten and Travis, 1968:696).

Diagnosis. Differing from all other South American chelids in having intergular scute withdrawn from anterior margin of carapace, and in hexagonal to octagonal shape of intergular; seven or eight pairs of scutes (in addition to an unpaired gular) on plastron, rather than six pairs; shell between fifty and one hundred per cent larger than that of *C. fimbriatus;* median ridge of carapace not increasing in prominence toward posterior end.

Description. Most of the specimens that I identify as *C. colombianus* are isolated shell elements. Owing to the distinctive shell morphology of *Chelus,* however, there is no doubt about the propriety of the generic identification. Only two of the specimens (UCMP 78762 and GMB 2085) actually preserve evidence of the diagnostic scute position and pattern, but nearly all are from large individuals. Because the beds in which they were found are all of essentially the same age, there is no reason to suspect that more than one species is represented.

Of the type, little is missing except at the anterior margin of the anterior plastral lobe. There has been some dorsoventral compaction of the shell, which has produced numerous cracks in the bone, especially on the carapace. Bone sutures can be clearly discerned on the plastron and, to a lesser extent, the boundaries of the peripheral bones can be delimited. So badly cracked is the central part of the carapace, however, that all traces of sutures have been obliterated from this sector. None of the other specimens, however, reveal any peculiarities in the pattern of bone sutures for this part of the carapace. No grooves demarcating the boundaries between adjacent scutes have been preserved on the dorsal surface of the carapace of the type, but most of the vertebral outlines can be detected in another specimen (GMB 2045A). No striking differences in vertebral proportions are evident. The proportions of the midline ridge provide the only possibily diagnostic character of the carapace; this ridge does not become increasingly prominent toward the rear of the shell, as is typically the case in the single living species. This feature by itself, however, would be insufficient to persuade me to recognize a new species, particularly in view of the fact that the limits of variation in the shell structure of the living species are so poorly known. In fact, except for the fortunate circumstance that parts of the anterior plastral lobe have been preserved in two specimens (the type and GMB 2085), there would be no compelling reason to suspect that the Colombian fossils represented anything other than overgrown examples of *C. fimbriatus.*

The scute pattern of the anterior plastral lobe is unique among chelonians in that one or two extra pairs of scutes were clearly present (Fig. 1). As the standard and heretofore invariable number of paired plastral scutes is six, these extra scutes have no counterpart elsewhere within the order.[1] The existence of these scutes does not seem to represent an abnormality as they were clearly present on both of the only two remains of anterior plastral lobes in the hypodigm. The derivation of these novel scutes is problematical. They may have grown in to fill the void left by the intergular scute as it withdrew from the forward edge of the plastron. If so, they might be termed the pre- or antegulars. But why supernumerary scutes should develop here in the case of *C. colombianus* but not in the case of the various living species of *Chelodina,* in which the intergular is similarly withdrawn, is not readily explicable. The extra pair of scutes might equally well have resulted from the anteroposterior subdivision of the humeral, pectoral, or abdominal scutes, in which case some other name would be more appropriate. Because of my uncertainty as to the homologies of the scutes on the front half of the plastron, I refrain from proposing a new name for the extra pair characteristic of this species. Disagreement about the nomenclature for the bones and scutes of chelonian shells is already widespread; the publication of almost every new monograph or book on turtles is usually an occasion for proposing a new name for some bone or scute, reviving one long disregarded, or reshuffling the standard terms to apply to elements not previously so named. This unsatisfactory situation can hardly be improved by introducing a new name arbitrarily assigned to any one of four pairs of scutes on the anterior half of the plastron. What is important is not the name of this pair of scutes, but their existence.

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[1] I know, however, of one example of *C. fimbriatus* (PCHP 38) in which the humeral scutes have nearly been fully subdivided into anterior and posterior portions (Fig. 2). Of all the chelonian specimens that have ever come to my attention, this is the only one I have seen exhibiting such a tendency. Perhaps it is atavistic.

Intergular scutes that do not enter into the anterior margin of the plastron are found elsewhere among the chelonians only in the related genus *Chelodina,* whose distribution is limited to parts of Australia and New Guinea (Goode, 1967:24, 36). Except in occasional specimens of *Chelodina siebenrocki* (sensu Goode, 1967:44), in which the forward tip of the intergular may appear truncated by reaching the plastral margin,[1] the intergular scute is invariably hexagonal in shape. Of the two specimens of *Chelus colombianus* in which the shape of the intergular can be determined, one (the type) displays the typical hexagonal configuration seen in *Chelodina* while the other (GMB 2085) is octagonal. Apparently the shape of the intergular in *C. colombianus* was somewhat variable, but in any case it differs from that of the living species *C. fimbriatus,* which is also characterized by a variably shaped intergular, but one that is usually either triangular or pentagonal (see, for example, Schmidt, 1966, fig. 2). The octagonal intergular shape is, to the best of my knowledge, unique. The scute furrows radiating out toward the margin of the plastron on the specimen having the octagonal intergular (GMB 2085) indicate that at least in some instances *C. colombianus* had an eighth pair of plastral scutes, again a unique condition among turtles. Clearly the number of pairs of supernumerary scutes (one or two) depended on the shape of the intergular and likewise was an individually variable feature.

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[1] In a series of fifteen specimens examined by my colleague A. Rhodin, one exhibited this atypical scute pattern (personal communication).

Accurate measurement of overall shell dimensions is possible only for the type. But a second, fairly complete and undistorted specimen (GMB 2045A) has been well restored and a reasonably reliable determination of its length and width is obtainable. When compared to a sample of shells of *C. fimbriatus* (Table 1), those of *C. colombianus* are obviously larger. The two measurable shells of the latter species were not exceptional representatives of the taxon since most of the fragmentary remains included in the hypodigm are of more or less the same size as comparable parts of the whole shells. Typical adult specimens of *C. colombianus* evidently were much larger than are those of its living congener.

Chelus lewisi sp. nov.[1]

Plates 4–5, Figure 3

Type. MCNC 239, a complete shell.

Hypodigm. The type, and MCZ 4337 and MCZ 4338, complete shells; MCNC 240, a pleural; MCNC 241, posterior half of a carapace and plastron; and MCNC 242, a crushed vertebra (probably a cervical) associated with a right xiphiplastron.

Horizon and locality. Urumaco Formation (Huayquerian), from several localities in the vicinity of the town of Urumaco, northwestern Falcón, Venezuela.

Specimens were collected at three different localities. The type was found just south of the oil pipe line running from Punta Gorda to the Paraguaná Peninsula, about .6 kilometer SW of where this conduit crosses the highway leading westward from Urumaco toward Maracaibo (National Route 3). A single specimen (MCNC 240) was encountered 3.5 kilometers NW of a hill known as El Picacho on the up side of the Chiguaje fault. The remaining material was all confined to a small area of exposures .4 kilometer SSW of Cerro Bacunare between the Valle de la Paz and Bacunare Faults.

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[1] I take great pleasure in naming this species for my good friend, Arnold D. Lewis, not only because he discovered the type specimen, but also in recognition of his many and varied contributions to the science of vertebrate paleontology over the years.

Diagnosis. Differing from other species of *Chelus* in marked posterior widening of carapace and in square rather than rectangular shape of the first neural bone. Shell 15 to 20 per cent larger than that of adult *C. fimbriatus.*

Description. Like most of the vertebrates from the Urumaco Formation, the specimens of *C. lewisi* are covered with a gypsiferous encrustation that has damaged the bone surface. The scute sulci have mostly been obliterated and it is possible to determine the full bone suture pattern in the type alone, and this only after weeks of painstaking preparation in the laboratory. Dimensions of the three complete shells are given in Table 1.

The distinctive shape of the carapace leaves no doubt about the validity of this taxon. The shells of both of the other species of *Chelus* are parallel-sided or nearly so,[1] whereas in all three of the complete shells of this species the width increases markedly from front to rear. Although each of these shells has undergone a varying degree of dorsoventral compaction, with the type showing the least amount of crushing, there is no evidence of significant lateral deformation and the present outline of the carapace is, I think, an accurate reflection of its true proportions in life.

The shape of the first neural bone also appears to be a distinctive feature of *C. lewisi.* Its length only slightly exceeds its width, and it is subrounded in outline, whereas in *C. fimbriatus* the length of this bone is generally much greater than its width, giving it a rectangular appearance (see Table 1 for measurements). The width/length ratio for *C. lewisi* (.92) is outside the range of values (.52–.84) for my sample of *C. fimbriatus* and well above the mean value (.69) for this species.[2] The six succeeding neural bones are indistinguishable from their counterparts in *C. fimbriatus.* The neurals are arranged in an uninterrupted sequence. Part of the seventh as well as all of the eighth pairs of pleurals meet in the midline of the carapace between the last neural and the suprapygal. This is the typical condition in many specimens of *C. fimbriatus.* Some variation, however, does occur in the living species (Table 1). A relatively small proportion of the carapaces in my sample (four out of nineteen) had eight rather than seven neurals. In all but one of these four specimens, the eighth neural abuts directly against the suprapygal, thus preventing any of the pleurals from meeting in the midline. In one specimen with only seven neurals, the neural series also extends continuously from the nuchal to the suprapygal so that no pleurals meet in the midline.

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[1] In some specimens of *C. fimbriatus* the sides of the carapace are actually bowed inwards slightly in the bridge region between the axial and inguinal notches.

[2] One specimen in my *C. fimbriatus* sample (PCHP 39) has a W/L ratio of 1.10. I have deliberately excluded this from consideration because its first neural has been transversely subdivided, thus resulting in clearly anomalous proportions (Fig. 4).

Outlines of three vertebral scute sulci (the second through fourth) can be detected on the carapace of the type specimen (MCNC 239), but otherwise none have been preserved on this or any of the other specimens referred to *C. lewisi.* The vertebrals are all proportionately broader than in a somewhat smaller specimen of *C. fimbriatus* (MCZ 4028; Table 2), but this may in part or entirely be due to dorsoventral compaction of the fossil, which is most pronounced in the middle of the carapace.

The smallest of the three shells of *C. lewisi* is nearly five centimeters longer than the largest of the available shells of *C. fimbriatus,* while the largest is slightly more than nine centimeters longer (Table 1). Hence it appears that typical individuals of *C. lewisi* were somewhat larger (15–20 percent) than their living congeners.

Aside from the proportions of the entoplastron, there is nothing exceptional about the shape or arrangement of the plastral bones. Entoplastral dimensions can only be determined for one specimen of *C. lewisi,* the type. For this individual, the greatest width of the entoplastron is only slightly less than its midline length, the width/length ratio being .93 (Table 1). Its proportions are such that it barely falls within the upper limits of the range recorded in Table 1 for similar measurements of *C. fimbriatus* (.50–.93). It may be that this bone tended to be relatively broader in *C. lewisi* than in the living species. If so, its proportions may prove to be a useful diagnostic character. However, until the range of variability in the dimensions of the entoplastron of *C. lewisi* is better known, judgment must be reserved regarding its diagnostic utility.

Another feature that may serve to differentiate *C. lewisi* from *C. fimbriatus* is the extent to which the three anteroposterior ridges on the carapace are developed. For all three of the complete shells of *C. lewisi,* the median ridge tends to be rather thin and only moderately undulating and, to a lesser extent, the same seems to be true of the lateral ridges. In the living species, the thicker median ridge becomes increasingly prominent toward the rear, whereas this does not appear to be the case for the Venezuelan fossils. These differences may to some degree be artifacts resulting from the dorsoventral compaction that all of the shells of *C. lewisi* have undergone. Although I suspect that they are indeed real, they are not vital for establishing the validity of the new species and therefore have not been mentioned in the diagnosis.

DISCUSSION

Up to now, the known fossil record for *Chelus* has been almost nonexistent. Although regrettable, this fact is hardly surprising, as the fossil record for South American chelids is in general abysmal. This rarity is somewhat puzzling, as the related pelomedusid turtles, forms that apparently have generally similar ecological requirements, are reasonably well represented in the vertebrate-bearing fossil deposits of the continent.

Fossilized remains were first referred to *Chelus* more than eighty years ago; these consisted of two shell fragments from the Amazon Basin of Brazil (Barbosa Rodrigues, 1892:48–49 and plates 12–15). They were recovered from beds that are of Pliocene or Pleistocene age along the course of the Rio Purus, probably not far downstream from the Peruvian border. The museum in which the specimens were apparently deposited no longer exists (Patterson, 1936:50) and the present disposition of these remains is unknown. Of the two fragments described by Barbosa Rodrigues, the more notable is a portion of the left xiphiplastron in which the distinctive elongation of the posterior tip, so characteristic of *Chelus*, has been preserved. Attribution of the two fragments to this genus was certainly justified. No species-specific characters are evident, however, and Barbosa Rodrigues showed commendable (and somewhat unusual) restraint for his times by simply designating them as *Chelys* (sic). Unfortunately, these specimens tell us nothing about the evolution of the genus, as they cannot be differentiated from comparable parts of the shell of the living species.

Subsequently, Wieland (1923:12–14) described a small portion of a carapace as representing a supposedly new species, "*Chelys*(?) *patagonica*." This specimen was of uncertain age and vague provenance — "Patagonian Tertiary beds (Miocene?)." Originally catalogued as part of the collections of the Peabody Museum of Natural History at Yale University, the fragment is now evidently misplaced or lost. Wieland should never have formally proposed a name for it. He was actually uncertain as to its proper generic allocation, suggesting that it might well belong to "*Testudo* [*Geochelone* in current terminology] or its allies," which I suspect might actually be the case since tortoise remains have been recovered from the Miocene of Patagonia (Simpson, 1942). Nor were any specific characters given for "*Chelys*(?) *patagonica*," which Wieland stated was ". . . a purely arbitrary name of convenience." By modern taxonomic standards it can only be regarded as a *nomen nudum* (see Simpson, 1942:2), and the specimen is of no further interest to the present study.

In 1956, while on a paleontological expedition to the upper reaches of the Rio Jurua, Dr. L. I. Price of the Geological Survey of Brazil discovered a very large plastron as well as a quantity of unassociated fragments that are all clearly referable to *Chelus*. These specimens are probably Plio-Pleistocene in age. None have so far been formally described, so I am uncertain whether they possess any distinctive characters other than exceptional size. It is possible that these remains represent a new species.

The two new taxa described in this paper represent the first valid extinct species of *Chelus* yet described. (They are also among the best preserved fossil chelids of any sort recorded from South America.) Unlike the Brazilian fossils mentioned above, both occur outside the present range of the living species.

Chelus at present occupies an enormous expanse of territory and yet remains a monotypic genus, much as the side-necked turtle *Pelomedusa* in sub-Saharan Africa. Unfortunately, relatively little is known about its ecology. Brief anecdotal comments have occasionally been published, but none of these, to my knowledge, are based on detailed or prolonged study of a single population or series of populations. The species is apparently not uniformly abundant throughout its range, nor does it appear to be especially common. Instead, populations seem to be scattered in ox-bow lakes and swamps along the banks of rivers. (This information was gleaned during the course of a paleontological expedition to Peru in the summer of 1974. Probably the species is distributed in a like manner throughout its range, but I cannot verify this.) Geological and faunal evidence associated with the discoveries of *C. colombianus* indicate that the ecology of this species was similar or even identical to that of *C. fimbriatus*. During Miocene times the area covered by the Villavieja Formation was a flood plain through which broad rivers and their tributaries meandered. Swamps, mud flats, and ox-bow lakes dotted the flood plain, which was periodically inundated. In general appearance, the area probably would not have differed appreciably from the wet, tropical zone of the present-day upper Amazon basin (Fields, 1957:279, 389–393). The habitat of *C. lewisi* is more difficult to reconstruct. This species is part of a fauna that consists predominantly of a variety of aquatic reptiles whose remains were buried in both continental and near-shore marine deposits (Wood and Patterson, 1973:2). Most or possibly all components of the fauna, however, were clearly nonmarine forms. Thus, it seems likely that *lewisi* was a nonmarine form, but it is unfortunately not possible at present to determine its habitat more precisely.

Both fossil species of *Chelus* possess characters that, I think, preclude them from the direct ancestry of *C. fimbriatus.* The intergular of *fimbriatus* borders on the lip of the anterior plastral lobe, as is the case for most turtles. But the recessed intergular scute of *colombianus* is an atypical chelonian feature, seen elsewhere only in certain Australian chelids. Hence, it is probably a derived rather than a primitive character for the genus. Since it is unlikely that a species with a derived character would later revert to the primitive condition, I suspect that these species are members of two distinct lineages. Both *colombianus* and *fimbriatus* have a carapace that is essentially parallel-sided; because this is characteristic of the oldest known and also of the only surviving species of *Chelus,* it seems to be the typical carapace shape for the genus. Thus I suspect that *lewisi,* with its posteriorly flaring carapace, represents a lineage divergent from that which gave rise to *fimbriatus.* Just as in the case of *colombianus,* it seems improbable that, in the course of evolution, a parallel-sided ancestral form could give rise to a flare-shelled species such as *lewisi* and then re-evolve the parallel-sided shell shape to give rise to the living species. It is conceivable that *colombianus* could have been ancestral to *lewisi,* but there are at present no compelling reasons to believe this. Whatever the relationships between these two species may have been, it now appears that there must have been a greater species diversity within the genus in the past, with several distinct lineages evolving in different directions at one time or another, only one of which has survived. Although its fossil record is still woefully fragmentary, it seems probable that *Chelus* has not always been a monotypic genus.

Part of the problem in dealing with fossil remains of *Chelus* is that so little is known about morphological variation in the living species. Certain variable features — the number of neurals and whether or not pleurals intervene between the last neural and the suprapygal — have already been noted. Other character variants of potential taxonomic importance also exist, notably the scute pattern on the anterior plastral lobe[1] and possibly also the proportions of the entoplastron. Schmidt (1966) has recorded additional ones: color patterns of the shell and extremities; shape of the intergular scute; morphology of the head; and relative width of the anterior plastral lobe. According to Schmidt, it is possible to recognize several subspecies of *C. fimbriatus* although he did not formally do so in his paper. This was just as well, as his sample was miniscule (five specimens) and the associated locality data were vague (e.g., "Brazil?", "Colombia", "Peru"). Nevertheless, it may indeed be possible to distinguish valid subspecies using some or all of the characters cited above, and perhaps others too. To do so, however, would require better collections than exist at present in museums, for several reasons. First, population samples from a single locality do not seem to exist, so that there is no basis for estimating the extent of intrapopulational variability. Second, the total number of specimens available for study appears to be rather small. And, third, variation in recent shells cannot be correlated with different parts of the species' range owing to the generally poor locality data associated with most museum specimens. For instance, ten of the nineteen specimens listed in Table 1 were obtained from zoos, identified simply as being from "South America," or were accompanied by no locality data whatsoever. Several others were labelled as being from the vicinity of Leticia or Manaus. These cities (as well as Iquitos) have long been the headquarters of professional animal collectors, and specimens brought to them may actually have been found far away. Only two had data good enough to permit identification of the river system in which they were captured, and even this is not entirely satisfactory as many tributaries of the Amazon and Orinoco Rivers are themselves hundreds of miles long. Considerable field work will therefore be necessary before it will be possible to determine convincingly whether or not valid subspecies of *C. fimbriatus* can be distinguished. Such field work would also have the added benefit of providing for the first time adequate knowledge about the ecology of this species.

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[1] Eleven of the nineteen specimens of *C. fimbriatus* recorded in Table 1 have the intergular completely separating the gulars. In an additional sample of eleven specimens, consisting of live individuals, juveniles, or shells for which I only have information about the relative positions of the scutes on the anterior plastral lobe, nine have the intergular fully intervening between the gulars.

TABLE 1

Some comparative measurements for the shells of *Chelus colombianus, C. lewisi,* and a sample of adult *C. fimbriatus.* All measurements are in centimeters. The symbol (?) means that features necessary for the determination of a particular character have not been preserved or, in the case of *C. colombianus,* that scute homologies are uncertain.

					First Neural				Entoplastron		
Species	Specimen No.	Midline Carapace Length	No. of Neurals	Parts or all of the 7th or 8th pairs of Pleurals meeting in midline	Length	Width	W/L Ratio	Intergular completely separating Gulars	Midline Length	Maximum Width	W/L Ratio
colombianus	UCMP 78762 (type)	54.8	?	?	?	?	—	?	10.2	8.2	.80
"	GMB 2045A	63[1]	?	?	?	?	—	?	?	?	—
lewisi	MCNC 239 (type)	45.5	7	yes	6.0	5.5	.92	?	7.0	6.5	.93
"	MCZ 4337	50[1]	?	?	?	?	—	?	?	?	—
"	MCZ 4338	46.7	?	?	?	?	—	?	?	?	—
fimbriatus	USNM 64154	39.9	7	yes	6.1[2]	3.6[2]	.59	yes	6.7	6.2	.92
"	USNM 65507	34.4	7	yes	5.3	3.7	.70	no	7.1	5.1	.72

"	USNM 8602	36.7	7	yes	5.8	4.1	.70	yes	7.2	5.6	.78
"	USNM 75323	23.7	7	yes	3.4[2]	2.3[2]	.68	no	5.0	2.5	.50
"	USNM 102883	35.6	8	yes	4.9[2]	2.9[2]	.59	no	7.8	5.0	.64
"	BMNH 1931.1.2.1	36.5	7	yes	5.1	4.2	.82	no	6.3	5.4	.86
"	BMNH 81.9.27.4	37.1	7	yes	5.5	4.3	.78	no	6.6	5.5	.83
"	MCZ 4028	31.1	7	yes	5.5	3.1	.56	yes	7.3	4.5	.62
"	AMNH 43298	39.8	7	yes	6.1	4.0	.66	yes	7.0	5.5	.79
"	AMNH 43305	37.9	7	yes	5.9	4.1	.69	yes	6.1	5.7	.93
"	AMNH 6596	>36[1]	7	yes	5.6	4.0	.71	yes	6.1	5.6	.92
"	AMNH 5911	38.3	8	no	6.1	4.8	.79	no	7.5	5.5	.73
"	AMNH 70638	38.4	7	no	6.6	4.1	.62	yes	7.0	6.0	.86
"	MZUSP 2019	40.4	8	no	6.1	5.1	.84	no	8.0	6.5	.81
"	MZUSP unnumbered	32.6	7	yes	4.8	3.4	.73	yes	5.4	4.8	.89
"	PCHP 36	34.0	7	yes	5.4	4.1	.76	no	7.9	4.5	.57
"	PCHP 37	31.8	7	yes	5.2	2.7	.52	yes	6.2	4.1	.66
"	PCHP 38	37.2	7	yes	5.7	3.8	.67	yes	6.5	5.9	.90
"	PCHP 39	33.7	8	no	2.9	3.2	1.10	yes	6.8	4.9	.72

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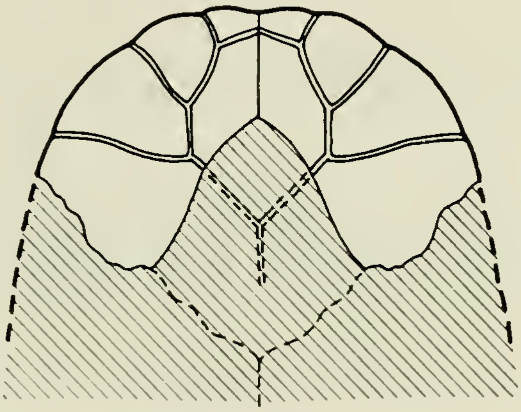
[1] estimated total length.

[2] measurements taken from the inside of shell. The proportions of a bone on the inside of a shell are known sometimes to vary from those on the outside. These, however, all fall within the range for measurements taken on the outside of the shell and have therefore been included.

TABLE 2

Dimensions (in centimeters) of the three vertebral scutes preserved on the type carapace of *Chelus lewisi* (MCNC 239) compared with those of comparable scutes of a specimen of *C. fimbriatus* (MCZ 4028).

Specimen number	MCNC 239			MCZ 4028		
Vertebral number	2	3	4	2	3	4
Midline length	8.5	8.9	8.0	6.6	5.9	5.1
Greatest width	12.4	13.1	10.4	7.1	6.9	6.3
W/L ratio	.69	.68	.77	.93	.86	.81



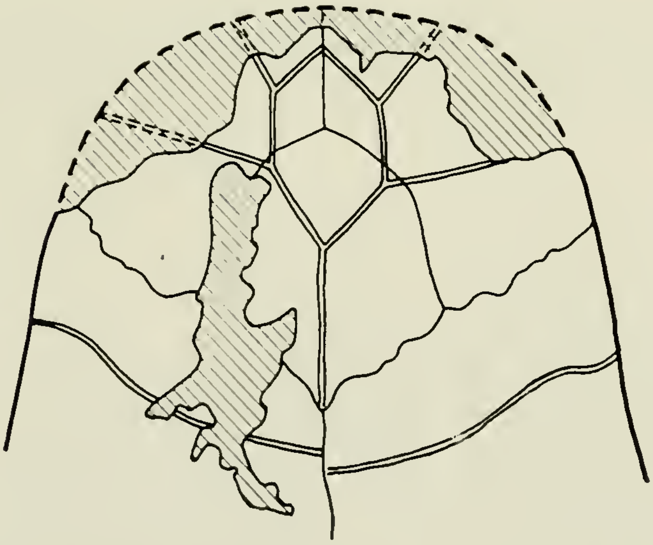


Figure 1. Scute patterns on the anterior plastral lobes of two specimens of *Chelus colombianus,* GMB 2085 (top) and UCMP 78762 (bottom). Compare with Figure 2 for an example of the typical scute pattern in *Chelus fimbriatus.* The right epiplastron of GMB 2085 has been restored as a mirror image of the left side. The specimens are not to the same scale but have been drawn so that the entoplastron in each is of the same length.

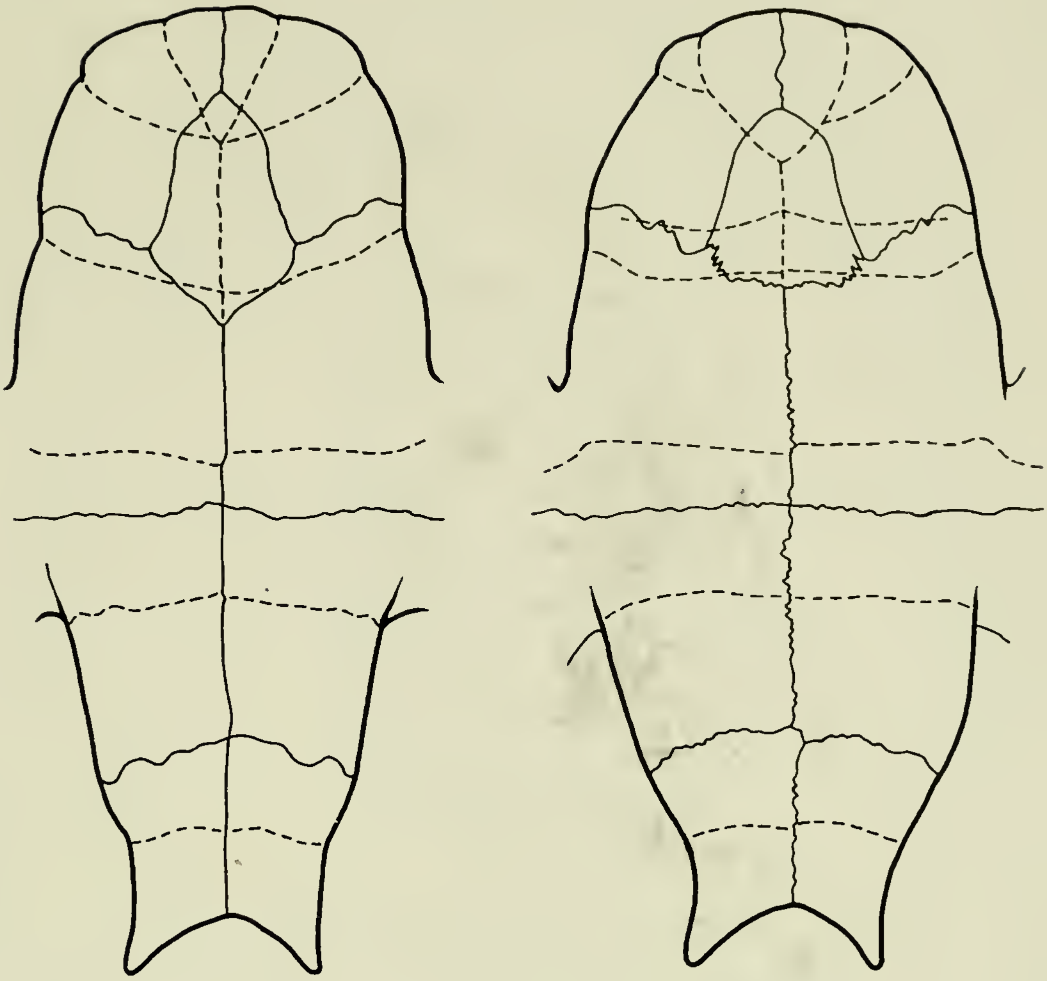


Figure 2. The plastron of a typical specimen of *Chelus fimbriatus* (MCZ 4028; left) and one (PCHP 38; right) in which the humeral scutes have nearly been fully subdivided into anterior and posterior portions. Both plastra are drawn to the same midline length.

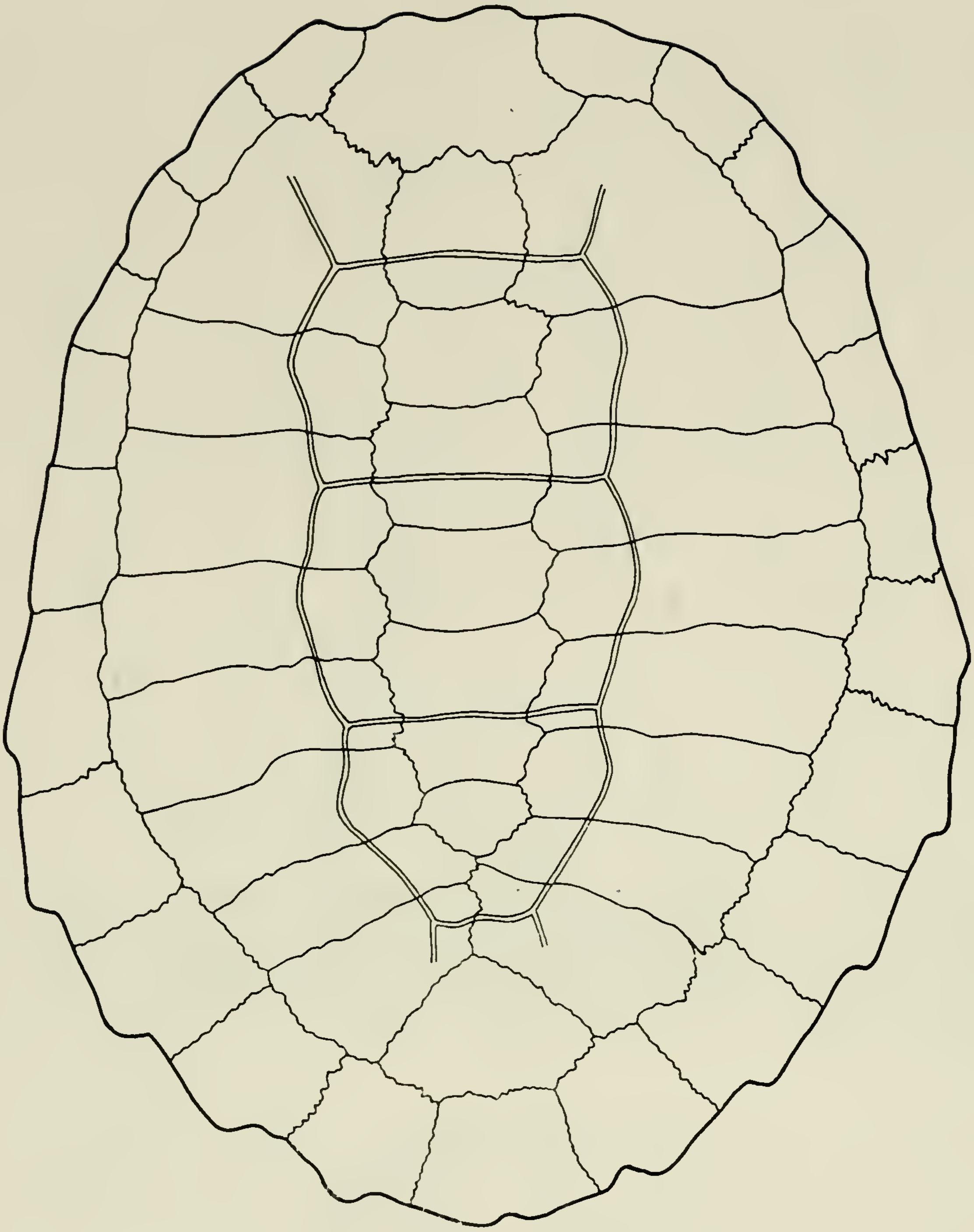
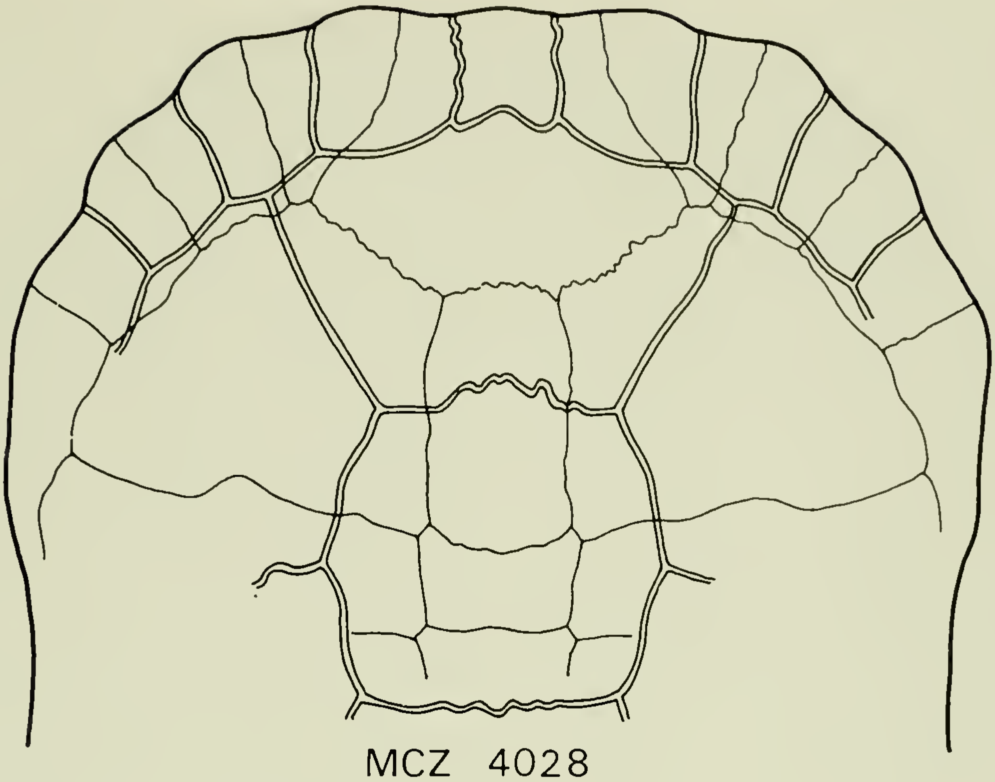
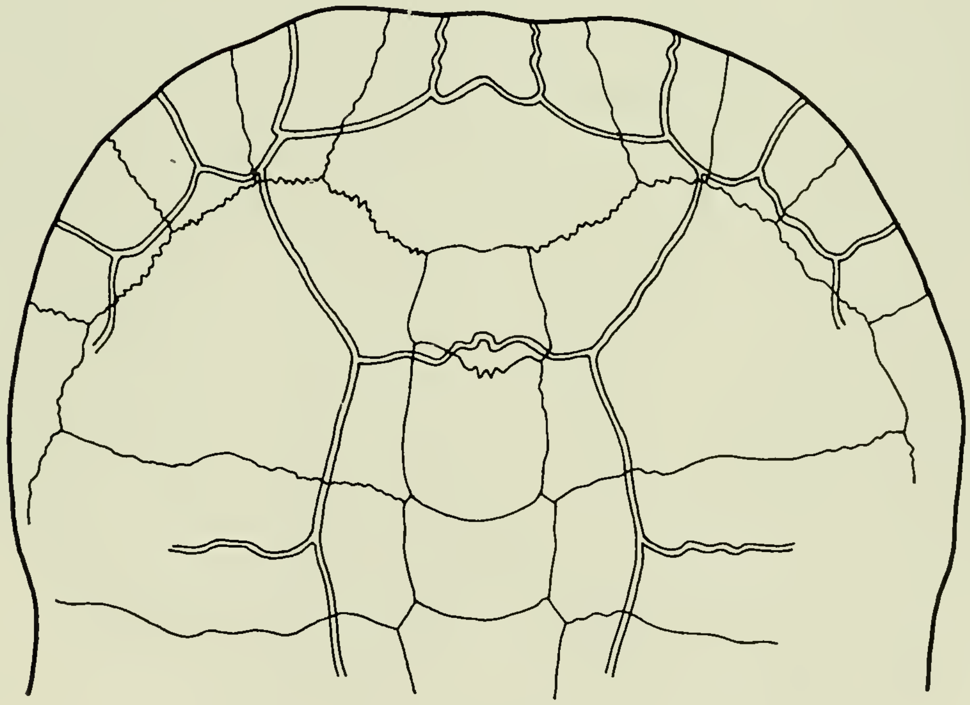


Figure 3. Sketch of the carapace of *Chelus lewisi* to show the pattern of bone sutures as well as those scute sulci that can be detected. Some compensation has been made for distortions resulting from the dorsoventral compaction of the specimen (compare with Plate 4).



MCZ 4028



PCHP 39

Figure 4. Anterior ends of two recent *Chelus fimbriatus* carapaces (not drawn to same scale) to show typical proportions of the first neural (top) and its abnormal subdivision (bottom).

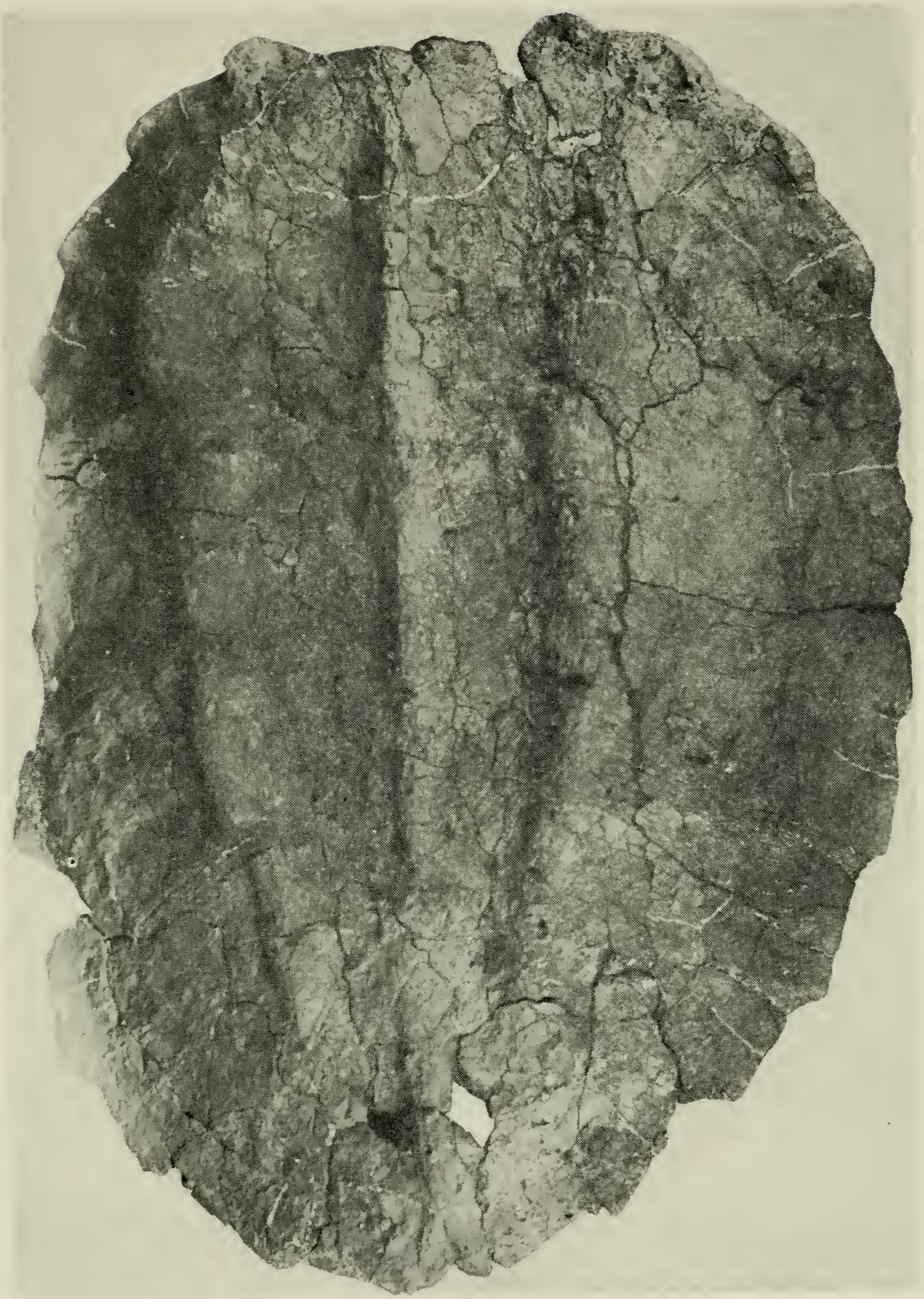


Plate 1. Carapace of the type specimen of *Chelus colombianus* (UCMP 78762). Its midline length is 54.8 cm.

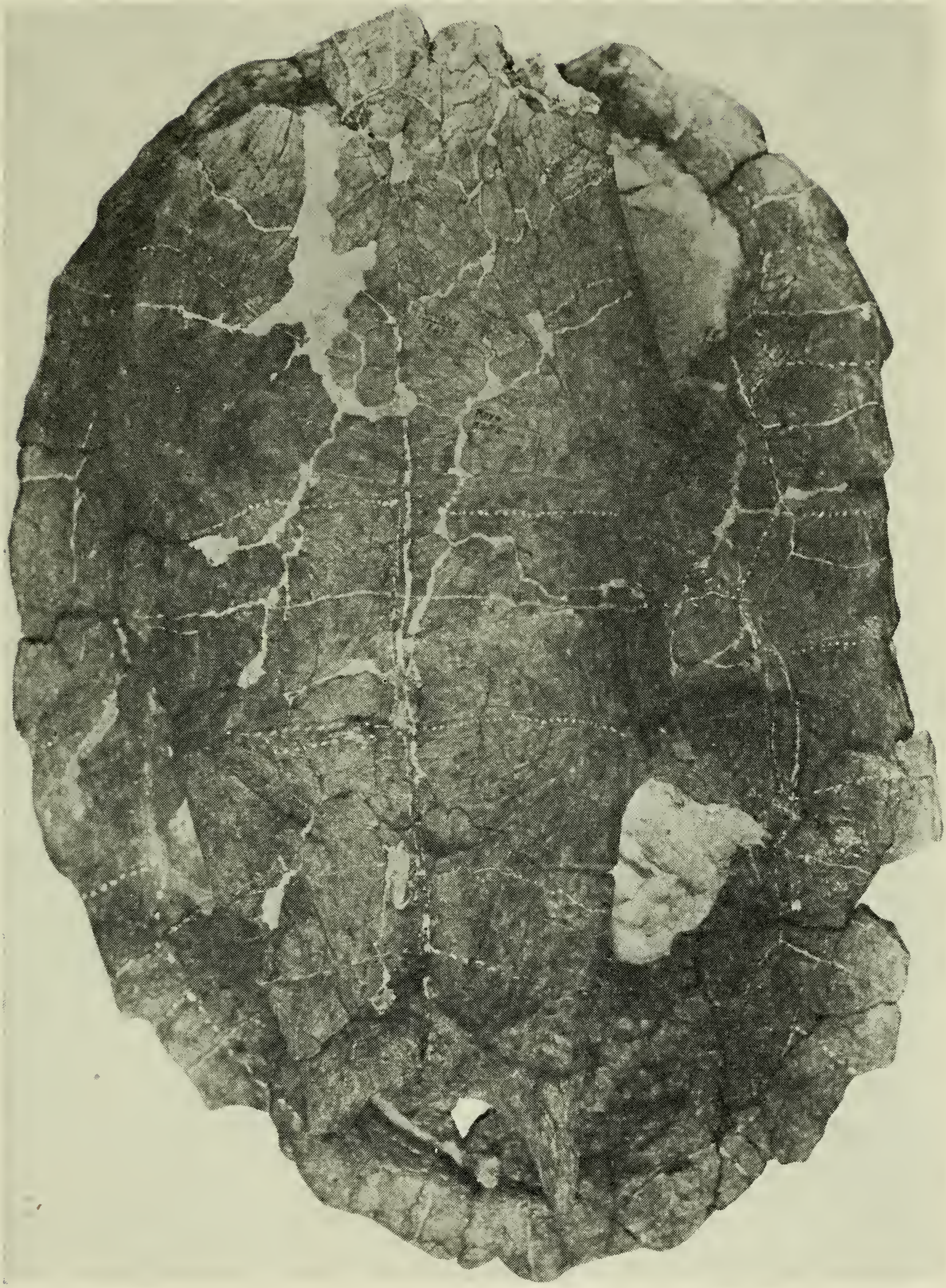


Plate 2. Plastron of the type specimen of *Chelus colombianus* (UCMP 78762).

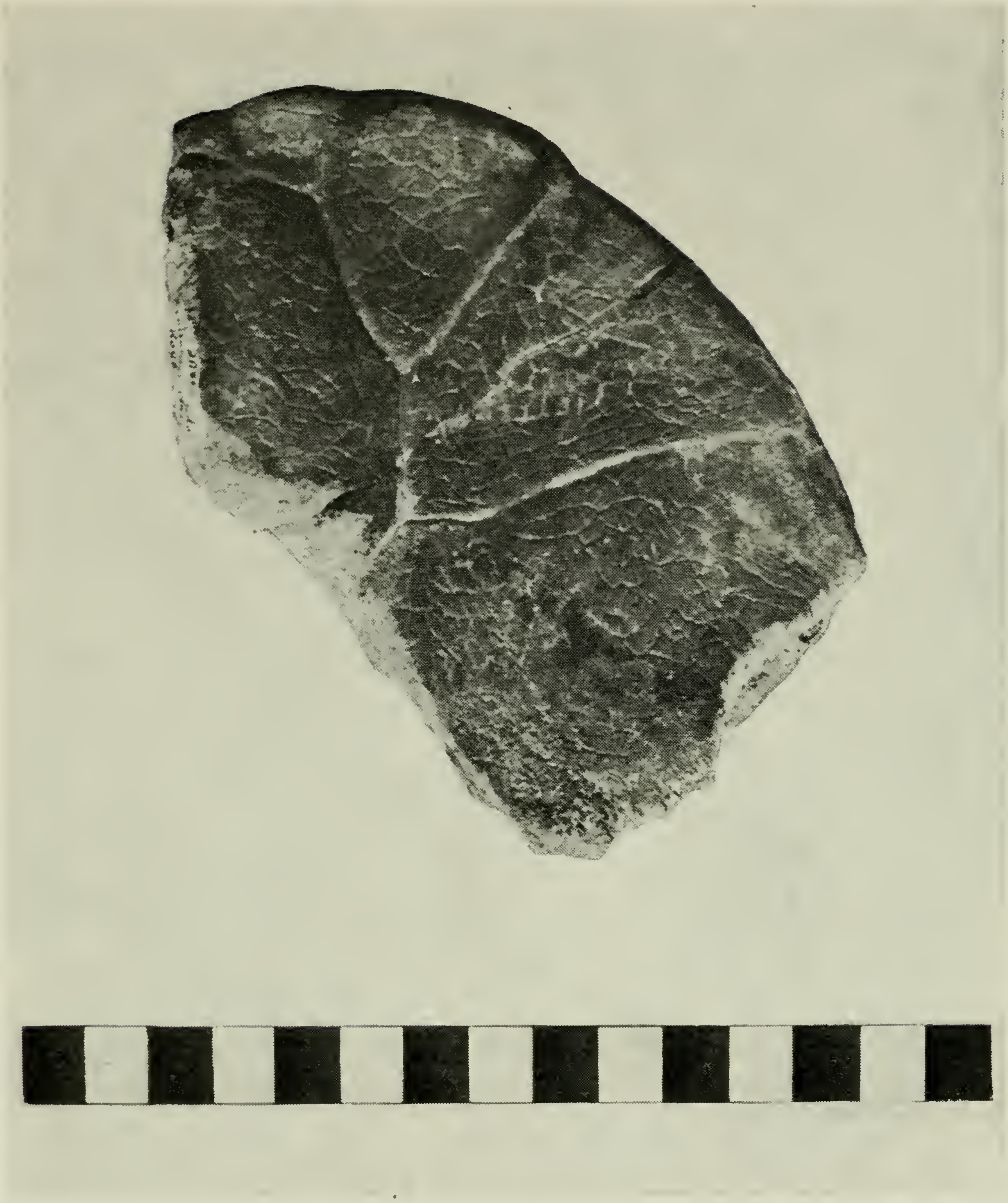


Plate 3. Left entoplastron (in external view) of a specimen (GMB 2085) referred to *Chelus colombianus.* The scale is in centimeters.

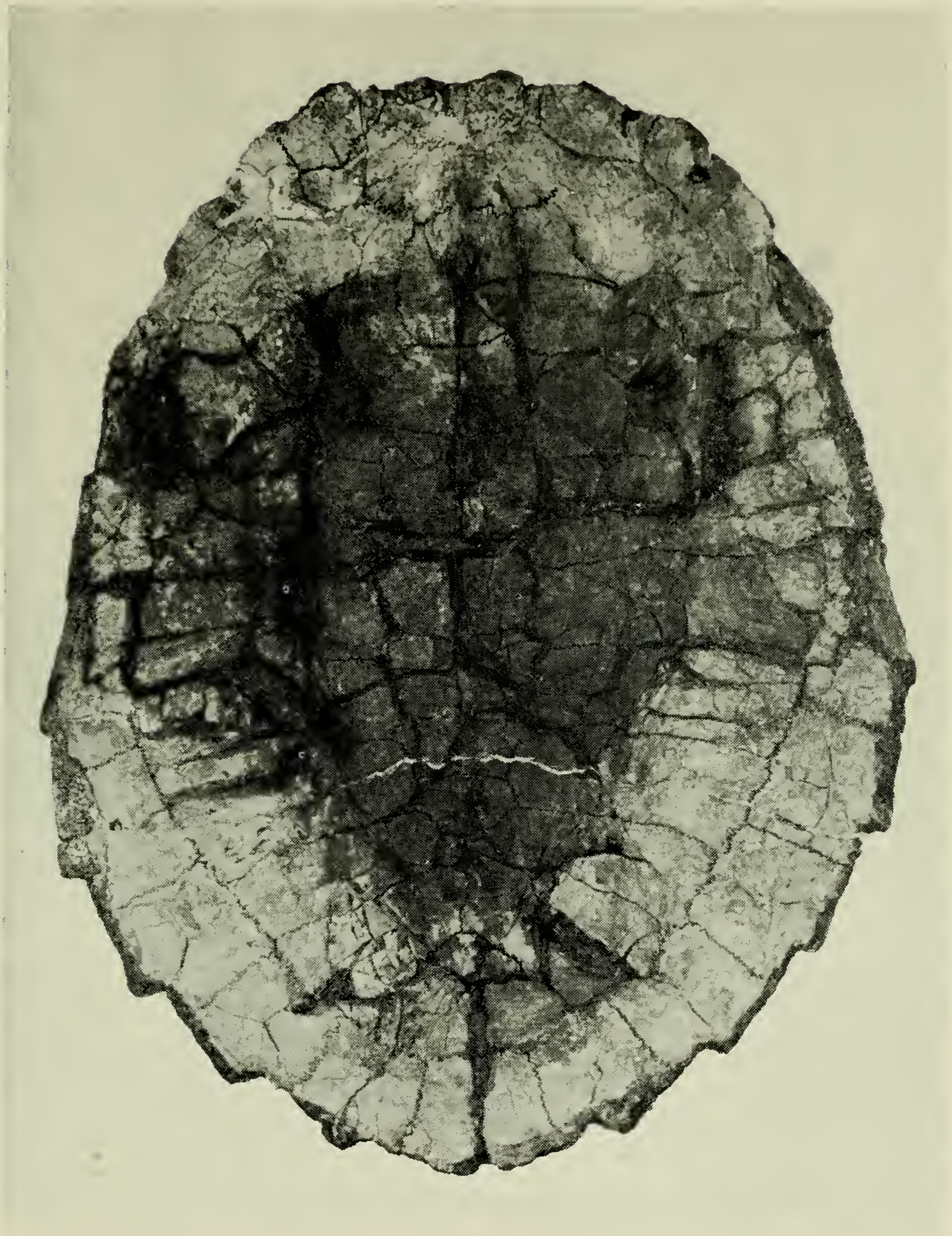


Plate 4. Carapace of the type specimen of *Chelus lewisi* (MCNC 239). Its midline length is 45.5 cm.

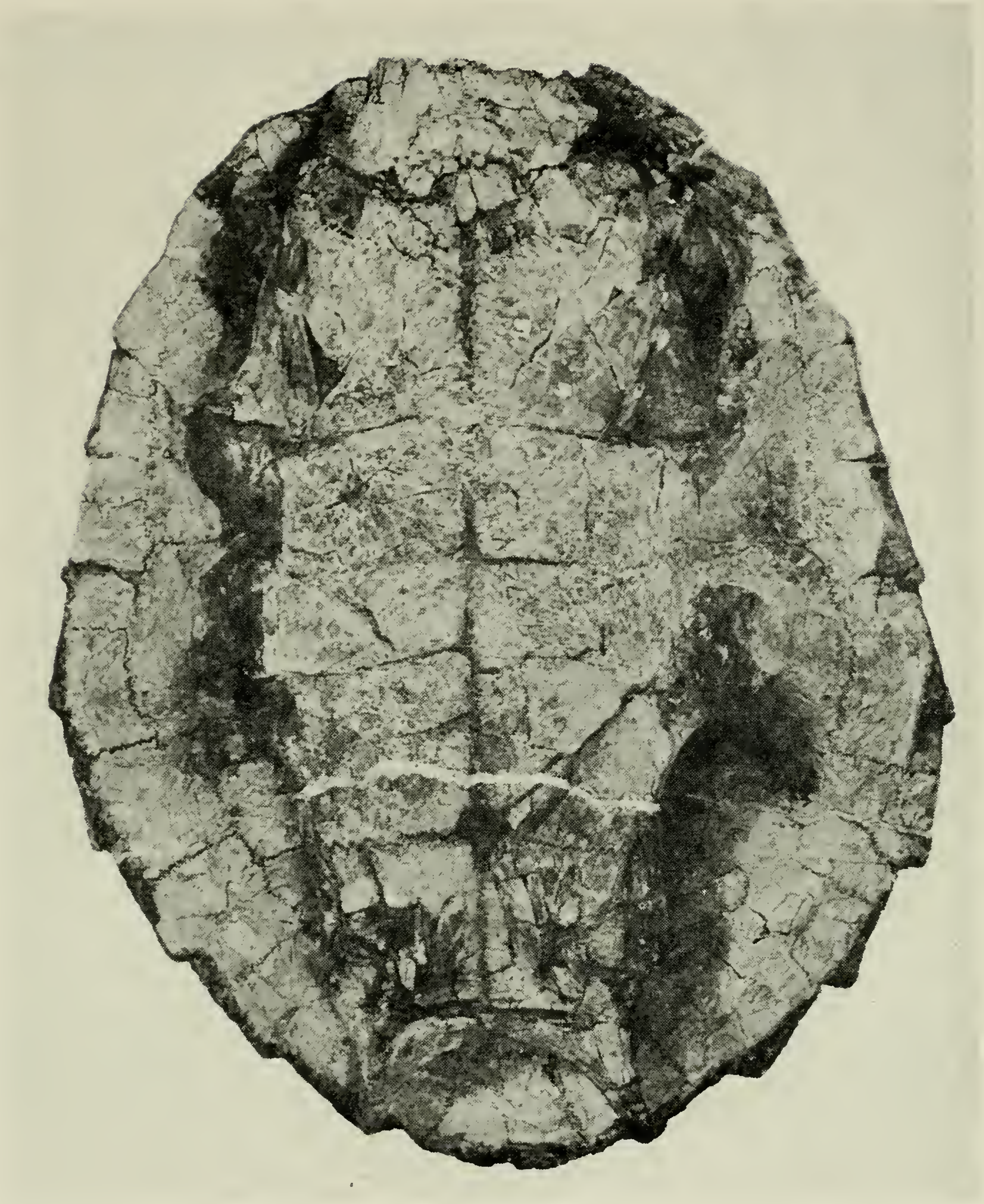


Plate 5. Plastron of the type specimen of *Chelus lewisi* (MCNC 239).

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STUPENDEMYS GEOGRAPHICUS, THE WORLD'S LARGEST TURTLE

ROGER CONANT WOOD[1]

ABSTRACT: *Stupendemys geographicus,* a gigantic fossil pelomedusid turtle from the late Tertiary (Huayquerian) Urumaco Formation of northern Venezuela is described. *Stupendemys* was evidently a highly aquatic form. Whether it was a fresh water or marine turtle, however, cannot be determined with certainty on the present evidence. One or perhaps even both pairs of limbs may have been modified into flippers, and the head may not have been fully retractable in the usual pleurodiran manner. Comparisons with records of other enormous chelonians reveal that the carapace of *Stupendemys* is larger than that of any other turtle, fossil or recent.

INTRODUCTION

Paleontologists are occasionally fortunate enough to make totally unexpected discoveries. Such was the case during the summer of 1972, when a Harvard paleontological expedition working in late Tertiary deposits of northern Venezuela unearthed the remains of several huge fossil turtles. These certainly attained greater size than any other extinct chelonians yet known; they also appear to be larger than any living ones and hence the largest turtles that ever existed. The purpose of this paper is to describe these gargantuan creatures.

The following abbreviations are used:

AMNH: American Museum of Natural History, herpetological collections
MCNC: Museo de Ciencias Naturales, Caracas
MCZ: Museum of Comparative Zoology: (H), herpetological collections; (P), paleontological collections
PU: Geology Museum, Princeton University

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SYSTEMATICS

Order Testudines
Suborder Pleurodira
Family Pelomedusidae

Stupendemys[1] gen. nov.

Plate 1 and Figures 1–3, 5, 6, and 9

Type species. *S. geographicus*[1] sp. nov.

Distribution. Huayquerian, Venezuela

Diagnosis. Shell gigantic; carapace depressed, with irregular nodular contours on external surface and deep median notch at front; anterior border of nuchal bone thickened and moderately to strongly upturned; posterior peripheral bones moderately scalloped along margins; neurals arranged in uninterrupted sequence, numbers two through six hexagonal, the seventh pentagonal. Mesoplastra hexagonal to subcircular, largely confined to bridge; lateral ends of pectoral-abdominal scute sulci terminating just anterior to axial notches of shell.

Cervical vertebrae (probably seventh and eighth) with saddle-shaped articulations; neural arches relatively high in relation to anteroposterior lengths of centra; angle of neural arch of presumed eighth cervical with horizontal plane greater than in any other pelomedusid; articular facets of postzygapophyses of both cervicals forming acute angle of less than ninety degrees with respect to each other; prezygapophyses of presumed eighth cervical directed more perpendicularly than in other pelomedusids; thin, bladelike spine on anterior face of eighth neural arch; no ventral keel on eighth centrum.

Angle of divergence between two ventral processes of scapulocoracoid roughly ninety degrees; ventromedial process of scapula dorsoventrally flattened; coracoid greatly thickened along medial edge; glenoid socket facing forward rather than laterally.

Humerus squat, massive, lacking ectepicondylar groove of foramen; deep bicipital fossa between radial and ulnar articular facets on ventral surface; prominent ridge traversing ventral surface of shaft from ulnar process to distal end, terminating just above radial condyle; ulnar condyle broadest at anterior end; ulnar and radial condyles facing somewhat more ventrally than in other pelomedusids; entepicondyle and supinator process strongly developed, resulting in distal expansion of humerus almost as great as that of proximal end; shaft triangular in cross-section rather than circular.

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[1] The generic name alludes to the astonishing size of this turtle, and the species is named in honor of the National Geographic Society in recognition of its generous support of my research on turtles.

Femur squat, massive, greatly flattened dorsoventrally; breadth of tibial condyle approximately one-third total length of bone.

Stupendemys geographicus sp. nov.

Type. MCNC 244, medial portion of the carapace with associated left femur, fragments of a scapulocoracoid and a cervical vertebra, probably the eighth.

Hypodigm. The type, and MCZ(P) 4376, much of the carapace, fragments of the plastron, a cervical vertebra (probably the seventh), both scapulocoracoids and a caudal vertebra; MCNC 245, a plastron lacking the epiplastra and entoplastron, two nearly complete pleurals, several peripherals, and one neural, all from the same individual; MCZ(P) 4377, a cervical, probably the eighth; and MCZ(P) 4378, a left humerus.

Horizon and localities. "Capa de huesos" (also known as "Capa de tortugas"), upper member of the Urumaco Formation, Huayquerian (which is probably of Pliocene age; see, for example, Simpson, 1974: 5).

Outcrops of the Urumaco Formation are restricted to a relatively small area in the northwestern part of the state of Falcón, centering around the now-abandoned El Mamón oil field (lat. 11°13′N, long. 70°16′W), just north of the town of Urumaco. The type was found immediately west of Quebrado Tio Gregorio, near its mouth. Other specimens were found as follows: MCZ(P) 4376 — one-half km north of Quebrado Picacho and 50 m east of the Chiguaje fault; MCZ(P) 4377 — three and one-half km north 30° west of El Picacho on the up side of the Chiguaje fault; MCZ(P) 4378 — as for the previous specimen, but about 15 m higher in the section; MCNC 245 — three-quarters km north of Kilometer 153 on the oil pipeline running from Punta Gorda to the Paraguaná Peninsula (same locality as MCNC 238, a trionychid; Wood and Patterson, 1973).

Diagnosis. As for the genus.

DESCRIPTION

Shell. The most complete carapace is that of MCZ(P) 4376 (Plate 1), which lacks some of the anterior peripherals on the right side, as well as peripherals from the bridge region on both sides. Scute sulci are deeply impressed onto the external surface but, as in many giant chelonians, most of the bone sutures have become largely fused and the pattern of these cannot be traced with any degree of certainty. The carapace is low-arched in the manner typical of aquatic turtles, and its dorsal surface, rather than being smooth, is somewhat nodose. There is a strong median indentation at the anterior margin of the carapace that is unique among pelomedusids (and perhaps even among turtles in general) in having the bone of this region curled up into a thickened, collarlike structure. Posterior to the bridges, the peripheral bones have mildly scalloped margins. The sacral region of this specimen is fairly well preserved. There are four sacral ribs abutting against the attachments of the ilia onto the visceral surfaces of the eighth pair of peripherals; the distal ends of the last two of these are fused together. This is essentially the same pattern as reported by Zangerl (1948: 30–31 and pl. 4, fig. 3) for the largest living South American pelomedusid, *Podocnemis expansa.* There is a slight posteromedial overlap of the iliac scars onto the suprapygal. Whether these also extended forward onto the under surface of the seventh pair of pleurals (and if so, to what extent) is uncertain because the course of the suture between the seventh and eighth pairs of pleurals cannot be determined. Measurements of this carapace are given in Table 1.

The carapace of the type specimen (Fig. 1) differs in several respects from that of the one just described and moreover provides information about the shape and arrangement of the neural bones not revealed by the more complete specimen. Measurements of the vertebral scutes of the two carapaces (Table 1) indicate that the type was somewhat larger, roughly by five per cent. Its midline length, therefore, would have been in the neighborhood of ten to twelve centimeters longer, giving an estimated midline length of as much as 230 centimeters. The curling and thickening of bone at the anteromedian indentation is less pronounced in the type than in MCZ(P) 4376. The outlines of six neural bones can be traced on this specimen. The pattern revealed is typical for South American pelomedusids; the last neural, which I believe to be the seventh, is pentagonal while those anterior to it (presumably the second through sixth) are hexagonal. The neurals, again typically, tend to become progressively broader in relation to their anteroposterior length toward the rear of the series (Table 2). As far as can be determined, the neurals were arranged in an uninterrupted sequence. Behind the last neural, part of the seventh and all of the eighth pair of pleurals meet in the midline.

An isolated neural bone from another specimen (MCNC 245) adds further information about the structure of the median part of the carapace. The bone is hexagonal and somewhat longer than broad (Table 2), indicating that it comes from the anterior part of the series. Because the first neural of pelomedusids is usually elongate and rectangular or oval, it seems reasonable to assume that the specimen in question is either the second or third. The bone was obviously in direct contact with neurals both to the front and rear. This reinforces the impression already given by the type carapace that the neural series was continuous, and, in fact, if the neural is actually the second rather than the third, proves the point. A notable feature of this neural is its exceptional thickness in proportion to its length and width; at various places around the periphery the bone measures 2.8, 2.6, and 2.4 centimeters dorsoventrally. In general, pelomedusid neurals tend to be proportionately much thinner. Although it is not feasible to measure the thickness of the individual neurals of the type carapace, it is possible to state that the carapacial bone does appear to be disproportionately thick, even for a turtle of such exceptional size. Perhaps the unusual thickness of the shell should be considered a diagnostic character of the taxon.

There is nothing remarkable about the carapace scute pattern of *S. geographicus*. It is virtually indistinguishable from that of any of the living South American pelomedusids which, except for minor variations, are all very similar.

No identifiable plastral remains are associated with the type specimen. However, the mesoplastra, hyoplastra, and right hypoplastron of MCZ(P) 4376 were recovered; these had been crushed down into and molded against the shallow bowl-shaped depression formed by the visceral surface of the carapace (the shell was found lying upside down) and unfortunately preserve little in the way of detail. Nevertheless, the presence of mesoplastra in conjunction with pelves that were clearly fused to the shell leaves no doubt that these gigantic turtles are pelomedusids.

The mesoplastra are relatively small, hexagonal to subcircular elements, laterally positioned and confined largely to the bridge. This is the standard configuration for all known living and fossil South American pelomedusids. On the basis of size and thickness, I have referred a fairly complete plastron and some miscellaneous carapacial fragments (MCNC 245; Fig. 2) to *Stupendemys.* Although very large by ordinary pelomedusid standards (Table 3), this plastron is relatively small in comparison to the carapaces described above. Presumably it represents a young adult. The forward portion of the anterior lobe is missing. This is regrettable because it is this part of the pelomedusid shell that is generally the most useful for taxonomic purposes. Nevertheless, some interesting characteristics are evident. The bridge is considerably longer at its base than the posterior plastral lobe (Table 3). The bone is exceptionally thick in proportion to its length and breadth. And, most notably, the lateral ends of the pectoral-abdominal scute sulci terminate just in front of the bases of the shell's axial notches, on the edges of the anterior plastral lobe. This position is in contrast to other South American fossil and recent pelomedusids in which these sulci typically meet marginal scute sulci on the forward third of the bridge, usually just in front of the anterior mesoplastral bone sutures. The plastral formula, insofar as it can be determined, is: femoral>abdominal>anal.

Axial skeleton. The three cervical vertebrae that have been recovered (MCZ[P] 4376, MCZ[P] 4377, and MCNC 244) belong to three different individuals and represent only two of the eight bones in the series. Measurements of these are given in Table 4. Because of the unique morphology of these vertebrae, it is difficult to be certain as to their positions in the series. In the cervicals of living pelomedusids, the neural arches become increasingly prominent from front to rear, that of the eighth always having the greatest height in relation to the length of the centrum (Table 4). The two morphologically identical fossil cervicals (MCZ[P] 4377 and MCNC 244) have neural spines that are, relatively, even more prominent than that of the eighth cervical in living pelomedusids, while the third (MCZ[P] 4376) has an arch only slightly less prominent (Table 4). On this basis it would seem likely that we are dealing with cervicals at the posterior end of the series, presumably the seventh (MCZ[P] 4376) and eighth (MCZ[P] 4377 and MCNC 244).

However, examination of the central articulations furnishes contradictory evidence. Cervicals four, five, and six of all living South American pelomedusids have saddle-shaped articulations, the seventh is similarly shaped anteriorly but convex posteriorly, and the eighth is concave in front and convex behind (Williams, 1950: 528, 532, 552, and fig. 11). The three known cervicals of *Stupendemys* have saddle-shaped articulations, and hence compare in this feature to the fourth through sixth cervicals of the extant South American pelomedusids, rather than to the seventh or eighth. (Undescribed fossil pelomedusid cervicals from the late Cretaceous of Brazil, which I have been able to examine through the courtesy of Dr. L. I. Price, are indistinguishable from those of living South American representatives of the family.) In living African pelomedusids, the centra of cervicals three through eight are uniformly procoelous (Williams, ibid.). Cervicals are known for only one African fossil pelomedusid (Wood, 1971), and these differ from both living African and South American forms in having articular surfaces intermediate in shape between the saddle joints of the latter and the procoelous condition of the former. No cervicals have been reported for fossil pelomedusids from continents other than Africa and South America, the only regions, together with Madagascar, where the family still survives. The cervical articulations of *Stupendemys* are therefore most closely comparable to those of its South American relatives.

Because the trend of anteroposteriorly increasing neural spine height seems to be consistent in all pelomedusids, whereas the pattern of cervical articulation varies somewhat, I am inclined to place more reliance in the former feature as a means for determining the relative position of the *Stupendemys* neck vertebrae in the cervical series. As Table 4 shows, the height/length ratio of the eighth cervical is always the greatest for any individual. Moreover, as shell size increases, the height/length ratio also increases, so that it is greater for the eighth cervical of *Podocnemis expansa* than for that of the much smaller *Pelomedusa subrufa.* Given these observations, and in view of the fact that the height/length ratios of MCZ(P) 4376 and MCNC 244 are considerably greater than those recorded for any of the Recent species, while that of MCZ(P) 4376 is about the same as the greatest ratio for the largest Recent specimen measured, it seems that the cervicals of *Stupendemys* are from the posterior part of the series, probably representing the seventh and eighth.

If the cervicals of *Stupendemys* are, in fact, the seventh and eighth, then they are unique among known pelomedusids by virtue of their saddle-shaped articulations. There are, in addition, several other features of these vertebrae that reinforce this impression. One of the most obvious is that the neural arch of the eighth cervical of *Stupendemys* makes a much less acute angle with the anteroposterior axis of the centrum than do those of the comparable cervical in other pelomedusids. (In the cervical series of Recent pelomedusids that I have examined, the neural arch of the eighth cervical always makes the greatest angle to the horizontal plane.) In posterior view, the articular facets of the postzygapophyses form an acute angle of less than ninety degrees with each other. Those of other pelomedusids are nearly horizontal to the dorsoventral axis of the vertebrae (fig. 4; see also Williams, 1950, fig. 11). Viewed laterally, the shafts of the prezygapophyses of the presumed eighth cervicals of *Stupendemys* are directed much more perpendicularly than those of other pelomedusids. Although impossible to measure precisely, the angle made with the horizontal plane in the specimens of *Stupendemys* seems to be roughly sixty to seventy degrees, whereas in others it is closer to thirty degrees (cf. figs. 3 and 4). The thin, median, bladelike spine on the anterior face of the neural arch of the presumed eighth cervical of *Stupendemys* is also unlike anything seen on comparable parts of other pelomedusid cervicals. In most pelomedusids, the ventral surfaces of the cervical centra are typically bowed upwards, sometimes quite strongly, along the anteroposterior axis. The one exception known to me is the eighth cervicals of South American representatives of *Podocnemis*. In these, a flat blade of bone projects downward from the ventral surface (Fig. 4). But in both examples of the presumed eighth cervical of *Stupendemys*, the ventral surface is neither bowed upwards nor downwards; it is, instead, flat. Unfortunately, the bottom of the presumed seventh cervical vertebra (MCZ[P] 4376) is too badly damaged to determine its original shape.

A single, small caudal vertebra was found in association with one of the shells (MCZ[P] 4376). It is poorly preserved and reveals no features of special interest.

Appendicular skeleton. Much of both scapulocoracoids have been preserved for MCZ(P) 4376, as well as fragments of one belonging to the type. It is not possible to determine with certainty the relative lengths of the three prongs making up the shoulder girdle. The medial tips of the ventromedial portions of the scapulae are broken off. The dorsal processes of this same bone have been broken at their bases and flattened into the same plane as the other two elements. Since their basal contacts have been obliterated, it is impossible to determine how much (if any) of these processes is lacking. The coracoids, however, appear to be complete. Both the left and right ones are of essentially the same lengths in MCZ(P) 4376 and are considerably longer than what remains of the ventromedial processes of the scapula, but slightly shorter than the more complete of the two dorsal scapular processes that have been preserved (Table 5). These proportions are in accord with those of Recent pelomedusids, in which the ventromedial process of the scapula is much shorter than the dorsal one, while the coracoid is intermediate in length, generally somewhat flattened dorsoventrally, and moderately to greatly expanded towards its extremity. Despite this incompleteness a number of distinctive features are evident. The glenoid socket faces almost directly forward in *Stupendemys,* whereas in typical pelomedusids it tends to face in a lateral direction (Fig. 5). The angle at which the two ventral prongs of the scapulocoracoid diverge is considerably less acute in *Stupendemys* than in any other known pelomedusid (Fig. 5). The shoulder girdle of *Stupendemys* further differs from those of typical Recent South American pelomedusids in that the ventromedial process of the scapula is dorsoventrally flattened. In specimens of *Podocnemis dumeriliana, P. expansa,* and *P. unifilis* that I have examined, this bone is anteroposteriorly flattened. The medial side of the coracoid of *Stupendemys* is greatly thickened. This is not true of the coracoids in living African representatives of the family, which are uniformly thin, flat, and greatly expanded. In typical South American pelomedusids as well as in *Podocnemis madagascariensis,* the coracoid is not so expanded but is transversely arched, with the apex of the arch on the dorsal side. (The one exception of which I am aware is *Podocnemis erythrocephala* [Mittermeier and Wilson, 1974]; the coracoid of this species does not expand at all towards its tip but remains uniformly oval along its entire length [e.g., MCZ(H) 10096].) The coracoid of *Stupendemys* may have been similarly arched, if the dorsoventral crushing of this element is taken into account. The thickness of bone along its medial edge, however, still seems to set it apart from the other South American forms. The dorsal scapular process in *Stupendemys* appears somewhat flattened, whereas in Recent pelomedusids it is more oval in cross-section. This flatness, however, may result from crushing in the horizontal plane; because of my uncertainty about this feature I have refrained from listing it as a diagnostic character.

A nearly complete left humerus (MCZ[P] 4378) is all that is known of the forelimb. This specimen is of great interest in that it is totally unlike the humerus of any other known chelonian — let alone pelomedusid — living or fossil. The head as well as the terminal portions of the radial and ulnar processes are missing, but otherwise the bone is complete (Fig. 6). This humerus is extraordinarily massive, with distal and proximal ends both markedly expanded, the latter slightly more so than the former (see Table 5 for measurements). The curvature of the shaft does not appear to differ appreciably from that of living pelomedusids. There is no trace of an ectepicondylar groove or foramen on the dorsal surface, a feature present in all other pelomedusids (and, indeed, chelonians in general). Between the radial and ulnar processes, on the ventral side, is a very deep, semicircular depression, the bicipital fossa. This is more prominent than in the fossil pelomedusid *Bothremys barberi* (Zangerl, 1948:34 and fig. 13; Gaffney and Zangerl, 1968) or *Podocnemis* but is developed to about the same extent as in *Pelomedusa* or *Pelusios*. Immediately above the articular facets on the ventral surface at the distal end of the shaft is a very deep, triangular fossa. This seems to be a natural depression rather than the result of poor preservation of the bone and has no equivalent, so far as I have been able to determine, elsewhere within the order. A thick, prominent ridge extends transversely across the ventral surface from the base of the ulnar process to a point adjacent to the radial condyle. Such ridges are absent in living pelomedusids, although less pronounced ones have been reported in fossil pelomedusids, *Bothremys* (Zangerl, 1948) and *Taphrosphys* (Gaffney, 1975; Fig. 8, this paper). Typically, the ulnar condyle in pelomedusids has a spool-shaped outline, equally expanded at both ends. The ulnar condyle of *Stupendemys,* however, is markedly broader at its anterior end than at its posterior limit. A further distinctive feature of *Stupendemys* is that the trochlea extends farther onto the ventral surface than in other pelomedusids. To either side of the trochlea, the supinator process and entepicondyle bulge outwards, the latter especially. Only in *Taphrosphys* is the distal end of the humerus expanded to such an extent (distal width over total length equals 0.47 in

Taphrosphys [Gaffney, 1975, p. 16], 0.44 in *Stupendemys*). In cross-section, midway between the ends, the shaft is triangular rather than circular or oval, as is typically the case for pelomedusids.

A left femur (Fig. 9) was found associated with the type shell. The head and terminal portions of both trochanters are missing, as well as some bone from an area at the distal end of the dorsal surface. The distal articular surfaces, however, have been largely preserved. If complete, the femur would have been of essentially the same length as the only known humerus (Table 5). Like the humerus, the femur of *Stupendemys* is massive. Its shaft is oval in cross-section and greatly flattened dorsoventrally. The shaft of *Podocnemis expansa* is also oval in coss-section but is instead flattened anteroposteriorly. As for the humerus of *Stupendemys,* the curvature of its femur does not seem to differ significantly from that of living pelomedusids. The distal end of the shaft is markedly expanded, much more so than in *Podocnemis expansa* (distal width over total length equals 0.47 in *Stupendemys,* 0.29 in *P. expansa* [MCZ(H) 4469]).

DISCUSSION

Stupendemys has many very unusual anatomical features. No modern chelonian is at all comparable to it, nor does it closely resemble any of the better known fossil turtles.

Its systematic position, at least, is clear: it is an aberrant member of the Pelomedusidae. This is conclusively demonstrated by several characters: 1) the presence of mesoplastra; 2) fusion of the pelvis to carapace and plastron; and 3) shape of the cervical articulations.

It is when one strives to understand *Stupendemys* as a living animal that difficulties arise. In the following pages I attempt a functional analysis of the known parts of the skeleton, searching for clues to behavior and habitat.

The relatively low-arched carapace of *Stupendemys* indicates that it was almost certainly a highly aquatic form, as are all living pelomedusids and most fossil ones. Pelomedusids (not yet formally described) from two different African fossil localities, one of Oligocene and the other of Miocene age, are the only terrestrial members of the family yet known (Wood, 1971). These forms had extremely high-domed shells, superficially very tortoiselike in appearance. Conversely, the only strictly terrestrial, flat-shelled turtle is the exotic pancake tortoise of East Africa, *Malacochersus,* and its shell structure represents an adaptation to most unusual habits. Shell shape thus seems to be a nearly infallible indicator as to whether a chelonian was aquatic or terrestrial, and *Stupendemys* clearly falls into the former category.

The strong median indentation at the front end of the carapace is not characteristic of pelomedusids in general, but is reminiscent of the condition seen in the unrelated, big-headed turtle, *Platysternon,* of southeast Asia. *Platysternon* has a very large head in proportion to the size of its shell; consequently, individuals of this genus are not able to withdraw their heads into the shell in the typical cryptodiran manner. But the anterior embrasure of the carapace provides a notch into which the back of the head fits when retracted to the maximum extent possible. The heavily boned dorsal roof of the skull then acts, in effect, as an anterior continuation of the carapace and evidently serves as a reasonably effective deterrent to predators. *Stupendemys,* too, may have had a proportionately large, heavily armored skull which did not have to be swung under the carapace for protection in the usual pleurodiran fashion, but instead was simply lodged against its anterior border when danger was imminent.

I cannot readily account for the significance of the thickened, curled-up bone at the anterior margin of the carapace. It might represent a variably-expressed secondary sexual character if the two carapaces in the available sample represent opposite genders. It has, so far as I am aware, no structural equivalent elsewhere within the order.

South American pelomedusids are the only chelonians having saddle joints on the articular surfaces of their cervical centra (Williams, 1950, appendix 1). But, as pointed out (p. 8), the cervical vertebrae of *Stupendemys,* although possessing the characteristic saddle joints, are in detail very different from those of any pelomedusid known from that continent or elsewhere. This fact supports the supposition that neck retraction in the genus was fundamentally different from that of other pleurodires. But if, as suggested above, *Stupendemys* was comparable to *Platysternon* in its ability to retract its skull only partially, then the similarities in behavior were not paralleled by structural resemblances of even the most superficial kind. The articular surfaces of the fifth through eighth cervical centra in *Platysternon* are generally doubled, the centra themselves are very broad and flat, the neural arches lack spines, and so on. In sum, while it is clear that the cervicals of *Stupendemys* are markedly different from those of any other known turtle, the significance of these differences is not readily apparent.

Regrettably, the relative sizes of the humerus and femur in *Stupendemys* cannot be determined with any degree of certainty. This is unfortunate because, for turtles in general, the proportions of the fore and hind limbs are good indicators of the customary mode of progression. Pelomedusids and most aquatic cryptodires rely primarily on their hand limbs for propulsion while swimming, hence their femora are larger than their humeri. But in tortoises and marine turtles, the opposite is true. Thus, for example, if it were possible to establish that the humerus of *Stupendemys* was larger than its femur, this might be taken as reasonably good presumptive evidence that this peculiar pelomedusid swam in a different way from all other pelomedusids — perhaps even with flipperlike appendages, as in the modern marine turtles. But direct comparisons between the humerus and femur of a single specimen of *Stupendemys* are impossible. Moreover, the only known humerus of *Stupendemys* was an isolated find, which therefore cannot be tied to shell size, so that even indirect comparisons (in which limb size is related to shell length) cannot readily be made.

Normally, limb structure is also a good index to the locomotory capabilities of turtles. The highly modified, flippered forelimbs of marine cryptodires have a humerus that tends to be broad, flat, and relatively straight-shafted. In aquatic (or largely aquatic) forms, such as the pleurodires and emydines, it is much more gracile, ordinarily more or less circular in cross-section, and with a moderate curvature of the shaft. Tortoise humeri are stout and often have a strongly bowed shaft. The humerus of *Stupendemys* does not fall satisfactorily into any of these broad categories. It is considerably more massive even than that of a tortoise, fairly straight in the shaft, but more circular than flat in cross-section. The heavy ridge across the ventral surface of the shaft almost surely provided an increased area for the attachment of hypertrophied antebrachial musculature. Such muscles would only be required if the distal extremity of the forelimb were for some reason disproportionately large, as in marine turtles. While admittedly tenuous, this line of reasoning leads me to suspect that the forelimb of *Stupendemys* was modified into a paddle, a structure highly efficient for swimming but ill adapted to a terrestrial existence of any sort. Given the absence of direct fossil evidence, however, this can only be a very tentative suggestion.

The humerus of the fossil pelomedusid *Taphrosphys* (Fig. 8; Gaffney, 1975, fig. 12) appears to be intermediate in structure between that of *Stupendemys* and those of typical representatives of the family. Unfortunately, the humerus is the only part of the forelimb of *Taphrosphys* so far known, so that this taxon provides no further insight into the structure and function of the *Stupendemys* forelimb.

Forms intermediate in femoral structure between *Stupendemys* and the typical pelomedusids (or turtles in general, for that matter) do not exist. Had the femur not been found in association with pelomedusid shell remains, its familial allocation would have been impossible. Differences between the femur of *Stupendemys* and that of a representative pelomedusid (*Podocnemis expansa*) have already been enumerated (p. 11). The strongly projecting trochanters, broad intertrochanteric fossa and flattened shaft of *Stupendemys* distinguish it readily from both marine cryptodires and tortoises, while the massiveness of the bone and the broad, flat shaft together differentiate it from that of the other aquatic forms. In these characters, in fact, together with the relative straightness of the shaft, the femur of *Stupendemys* is more like the forelimb of marine turtles than anything else. For this reason it is tempting to speculate that the hind limbs of *Stupendemys* may have been modified into paddling flippers as large as those possibly present on its forelimb.

In sum, the available anatomical evidence demonstrates that *Stupendemys* was an aquatic form. In all likelihood, one or perhaps even both pairs of limbs were modified as flippers. The very size of its shell suggests that *Stupendemys* must have inhabited large, permanent bodies of water which it probably left only to lay eggs. Among living aquatic turtles in general, the larger the species, the less likely it is to come out of the water except for nesting. Size alone probably prevented *Stupendemys* from basking along shores. Flippers, if it had them, would have made such an undertaking even more awkward. I suspect that *Stupendemys* was largely if not entirely herbivorous, again simply because of its size; all of the largest living turtles — land tortoises as well as the marine forms — are totally (or nearly totally) herbivorous.

Geological evidence, although often helpful in attempting to determine the habitat of a fossil, is, in the present case, equivocal. A variety of different facies are represented in the upper member of the Urumaco Formation, including near-shore marine, brackish, and fresh water deposits. Some of these fresh water facies consist largely of platy concretion zones, which are probably best interpreted as representing small ephemeral ponds. Root casts and locally abundant leaf impressions are also characteristic of these deposits. Mammalian remains (especially very large rodents) tend to be more abundant here, as are certain of the reptiles (e.g., *Chelus,* nettosuchids). Other fresh water deposits probably represent stream channels and, in some cases, swampy areas (as evidenced by localized accumulations of vegetable debris). In general, the vertebrate-bearing sediments were evidently laid down in a coastal area over which the position of the shoreline fluctuated back and forth repeatedly. *Stupendemys* could thus have been a marine form that washed up on a barrier beach or was stranded in the lagoonal waters behind one. Or it may have been a fresh water form carried to the delta of a large river system and buried there. Since the associated fossil fauna has strong Amazonian affinities and is deficient in typical marine components, the latter possibility seems strong. But all of the largest known aquatic turtles, both living and fossil, are marine forms. This fact, coupled with the fairly convincing presumptive evidence that a number of other fossil pelomedusids were marine forms,[1] prevents categorical rejection of the idea that *Stupendemys* may have been a marine turtle.

The largest of the living pelomedusids (all of which are fresh water forms) is *Podocnemis expansa,* which has a wide distribution throughout much of the Amazon and Orinoco River basins of South America. This species is sexually dimorphic, the females growing to much larger adult size than males (Ojasti, 1971). In a large sample taken from the Orinoco River over a period of several years, the maximum carapace length for a male was 51 centimeters whereas that for a female was 81 centimeters (J. Ojasti, personal communication). The largest shell of this species yet reported is 82 centimeters long (Williams, 1954: 293). Presumably this record is of a female, although the sex of this particular specimen was not indicated. With the exception of *Stupendemys,* no known fossil pelomedusids exceed *Podocnemis expansa* in size, nor do representatives of the only other known family of side-necked (pleurodiran) turtles, the Chelidae, ever approach *P. expansa* in size. Thus *Stupendemys* is by far the largest pleurodire, living or fossil, yet known.

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[1] Included among these are several species of *Taphrosphys* (Schmidt, 1931; Gaffney, 1975; Wood, 1975), *Bothremys* (Zangerl, 1948; Gaffney and Zangerl, 1968), and a generically indeterminate form from Puerto Rico (Wood, 1972). All of these were found in near-shore marine sediments, generally under circumstances such that they cannot reasonably be regarded as exotic elements washed in from a nonmarine environment.

A few species of living fresh water cryptodiran turtles attain greater carapace lengths than *P. expansa,* but none are reliably known to approach the size of *Stupendemys.* A length of nearly 130 centimeters has been recorded for the carapace of the Asiatic trionychid *Pelochelys bibroni* (Pope, 1935). Another Asiatic soft-shelled turtle, *Chitra indica,* is generally believed to have a maximum carapace length of approximately 90 centimeters. One unsubstantiated report indicates that *Chitra* may occasionally reach a carapace length of roughly 180 centimeters (Pritchard, 1967:211). No other living or fossil fresh water cryptodires as large as either of these recent trionychids are known.

Some other fossil cryptodiran turtles of enormous size have been described, but none of these had shells as large as those of *Stupendemys. Archelon ischyros,* from the Cretaceous of North America, is the largest of the fossil marine turtles; its straight-line carapace length is 193 centimeters (Wieland, 1909). When first described, *Geochelone atlas* (originally and rather appropriately named *Colossochelys*) was believed to reach twelve feet in carapace length (Falconer and Cautley, 1844). This estimate was based on composite reconstructions of fragmentary material and has subsequently been modified to a maximum of six feet (roughly 180 cm; see Lydekker, 1889, and Auffenberg, 1974: 173). None of the specimens that have since been referred to *G. atlas,* which is now known from the Pleistocene of India, Burma, Java, Celebes, and Timor (Hooijer, 1971; Auffenberg, ibid.), appears to have reached or exceeded this length. One or more species of *Geochelone* from the Pleistocene of Florida and Texas may also have attained similarly gigantic dimensions (W. Auffenberg, personal communication). However, no tortoises — living or fossil — ever seem to have grown any larger.

In fact, of all known turtles, only the anatomically peculiar marine turtle *Dermochelys coriacea* may rival *Stupendemys* in size. *Dermochelys,* commonly referred to as the leatherback, is reputedly the largest of all turtles, living or fossil. Adults consistently attain carapace lengths of over 150 centimeters (Pritchard, 1971). In the only large series of measurements ever made, involving 1500 mature female specimens encountered laying eggs on the beaches of French Guiana over several field seasons, the maximum length recorded was 180 centimeters (three individuals; P. C. H. Pritchard, personal communication). Larger specimens have occasionally been reported, up to a supposed length of 3.35 meters, but these are unusual and suspect because they are probably based on estimates rather than actual measurements (Carr, 1952:446), and, as Brongersma (1968:38–39) has noted, estimates of the sizes of free-swinging marine creatures generally tend to be greatly exaggerated. Thus, there do not seem to be any reliable records of leatherbacks that equal or exceed *Stupendemys* in carapace length. On the average, certainly, carapace lengths of *Dermochelys* are significantly shorter than those of *Stupendemys*. Moreover, if the known specimens are typical representatives of *Stupendemys*, then adult populations evidently tended to be significantly larger than those of *Dermochelys* are today. In sum, it is clear that *Stupendemys* is unquestionably larger than any other previously described fossil turtle and it also appears to be larger than any living species. *Stupendemys*, therefore, is the largest turtle that ever lived.

TABLE 1

Measurements (in cm) for carapaces of *Stupendemys geographicus*. Dimensions are given as straight-line distances rather than over the curvatures of the shells.

		MCNC 244	MCZ(P) 4376
midline length (as preserved)		184	218
total midline length		approx. 230	218
maximum width (estimated)		190-195	185
maximum parasagittal length		250	235
first vertebral	length	37.1	34.5
	width	approx. 26	approx. 24
second vertebral	length	33.5	34.0
	width	36.4	32.7
third vertebral	length	33.3	32.4
	width	39.3	34.4
fourth vertebral	length	39.3	37.8
	width	approx. 34	28.1
fifth vertebral	length	—	52.4
	width	—	51.7

TABLE 2

Neural bone measurements (in cm) for specimens of *Stupendemys geographicus.*

Specimen No.	Neural No.	Midline Length	Maximum Width	Width/ Length
MCNC 244	3	16.3	14.8	.91
”	4	16.6	19.2	1.16
”	5	15.5	18.0	1.16
”	6	11.7	19.0	1.62
”	7	11.4	14.9	1.30
MCNC 245	2 or 3	7.7	6.5	.84

TABLE 3

Measurements (in cm) of the plastron (MCNC 245) referred to *Stupendemys geographicus.*

midline length (as preserved)		57.2
total midline length (estimated)		76
width at axial notch		34.0
width at inguinal notch		35.3
anteroposterior length of bridge	left side	35.2
	right side	36.2
midline length of posterior lobe		21.0
parasagittal length of posterior lobe (to tips of xiphiplastra)	left side	25.2
	right side	25.5

TABLE 4

Measurements (in cm) of the cervical vertebrae of *Stupendemys* compared with those of adult representatives of each of the three living pelomedusid genera. (MCZ [H]4469, *Podocnemis expansa;* AMNH 10065, *Pelusios subniger;* MCZ[H]146146, *Pelomedusa subrufa*).

Specimen No.	Midline Carapace Length	No. in Cervical Series	Midline Length of Centrum	Height of Neural Arch Spine above Base of Posterior End of Centrum	Height/ Length
MCZ(P)4376	218	7(?)	9.0	13.4[1]	1.49
MCZ(P)4377	?	8(?)	9.0	15.1	1.67
MCNC 244	230	8(?)	10.8	18.7	1.73
MCZ(H)4469	72.2	5	3.1	2.8	0.90
"	"	6	3.5	3.3	0.94
"	"	7	3.6	4.1	1.14
"	"	8	2.7	3.9	1.44
AMNH 10065	24.2	5	1.3	1.1	0.85
"	"	6	1.3	1.2	0.92
"	"	7	1.6	1.5	0.94
"	"	8	1.5	1.5	1.00
MCZ(H)146146	12.8	5	1.0	0.6	0.60
"	"	6	1.0	0.7	0.70
"	"	7	1.1	0.8	0.73
"	"	8	1.0	0.9	0.90

[1] The bottom of the posterior end of this centrum is somewhat damaged so that a precise measurement is impossible; the figure recorded here is an estimate.

TABLE 5

Measurements (in cm) of the known appendicular skeletal elements of *Stupendemys geographicus.*

SCAPULOCORACOID (MCZ[P]4376)		
lengths (as preserved) of dorsal processes of scapulae	left:	36.2
	right:	39.7
lengths (as preserved, along anterior edge, starting from lateral side of glenoid fossa) of ventromedial prongs of scapulae	left:	25.3
	right:	26.9
lengths of coracoids	left:	37.0
	right:	36.9
HUMERUS (MCZ[P]4378)		
length (as preserved)		31.0
estimated total length		34
maximum width of proximal expansion (as preserved)		18.0
maximum width of distal expansion		15.0
dorsoventral width at middle of shaft		8.3
anteroposterior width at middle of shaft		6.4
combined widths of ulnar and radial condyles on ventral surface		10.1
FEMUR (MCNC 244)		
length (as preserved)		29.5
estimated total length		33–34
maximum width of distal expansion		15.7
dorsoventral width at middle of shaft		6.5
anteroposterior width at middle of shaft		8.0

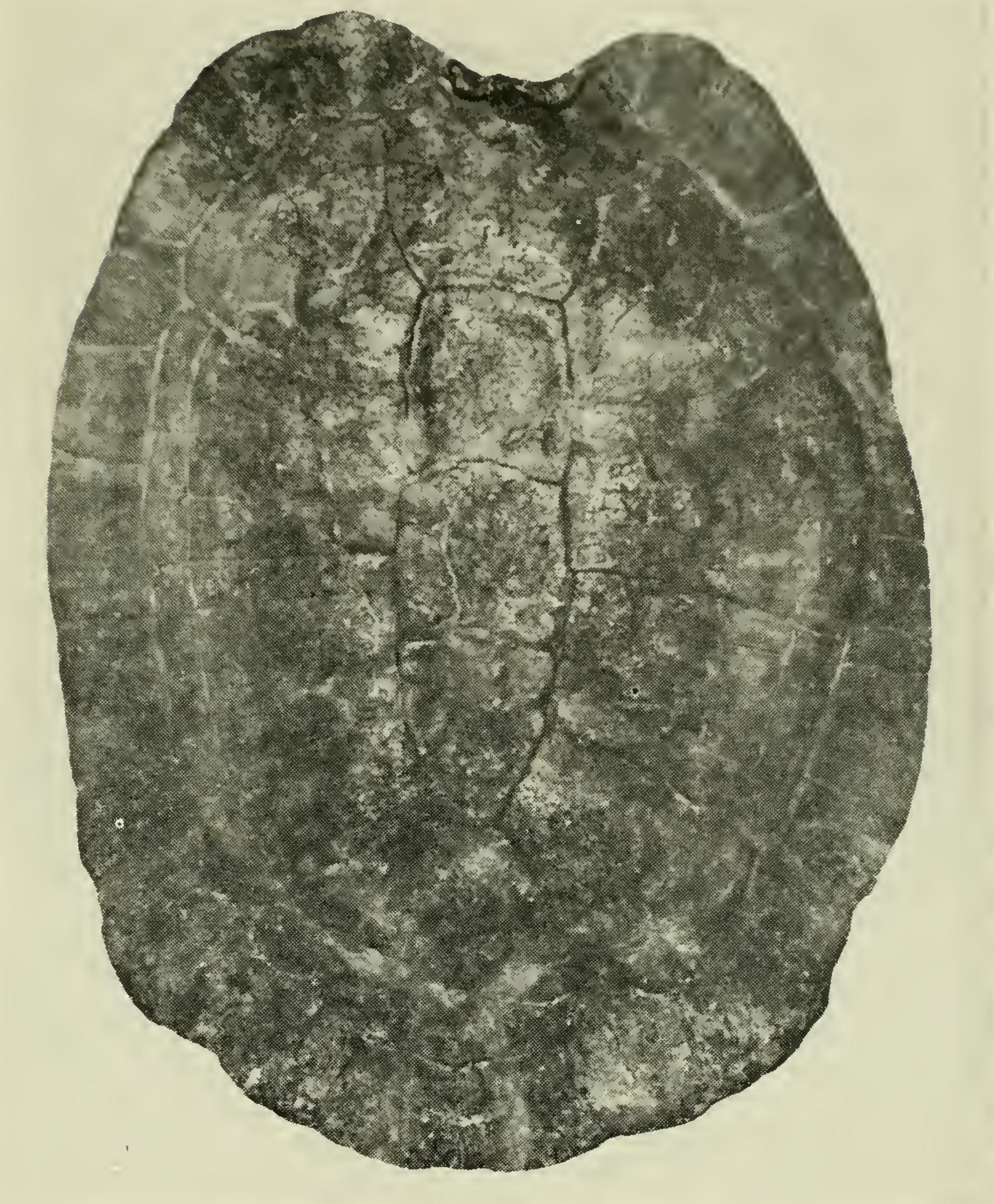

Plate 1. The carapace of *Stupendemys geographicus* (MCZ[P]4376), in dorsal view. Note especially the strongly curled bone at the base of the antero-median indentation. Midline length of this specimen is 218 cm. Peripheral bones in the region of the bridge on both sides, some of the more anterior peripherals on the right, and the lateral ends of some of the pleurals have been restored.

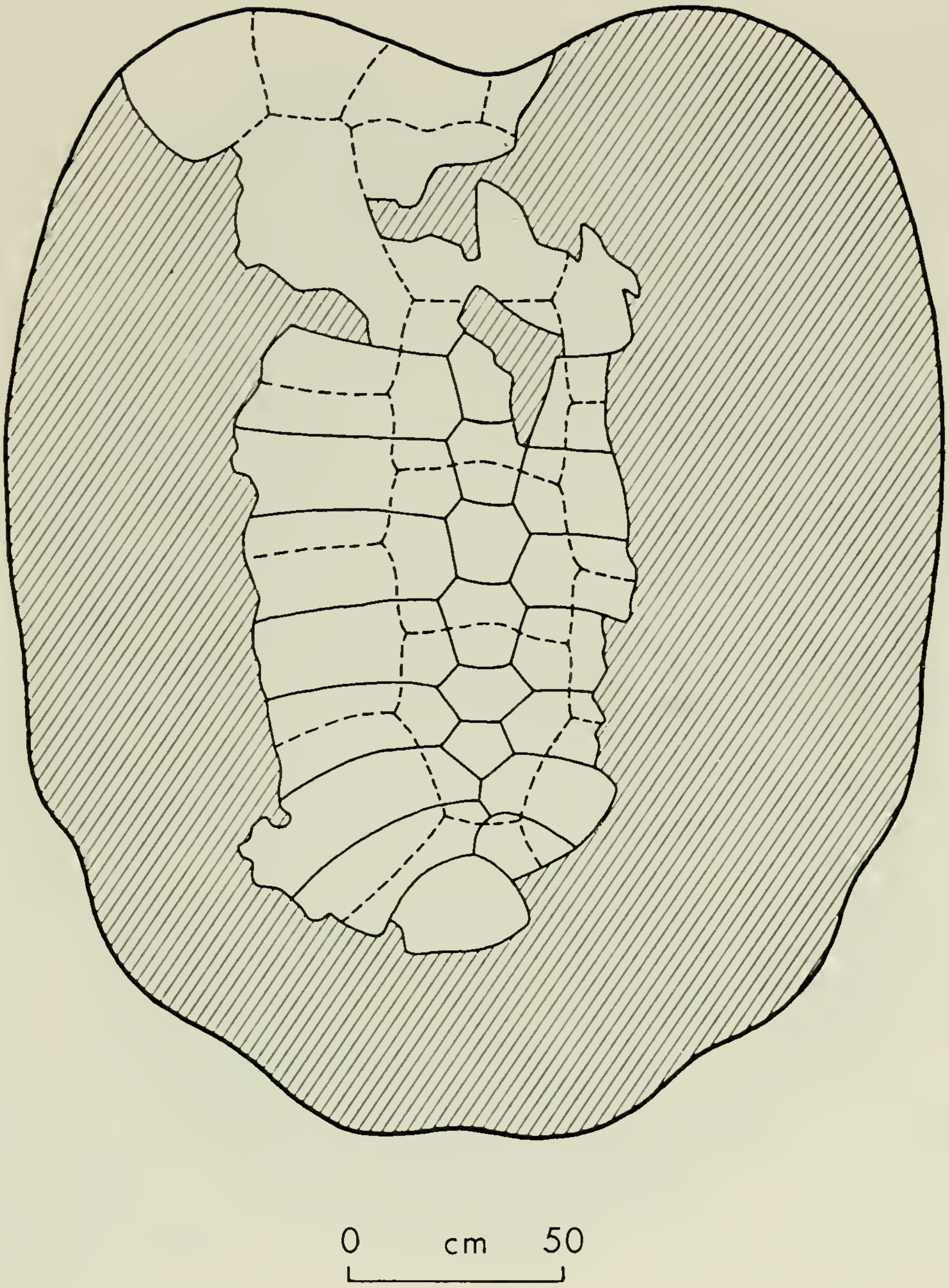

Figure 1. Carapace of the type of *Stupendemys geographicus* (MCNC 244) showing the shapes and positions of the second through seventh neural bones.

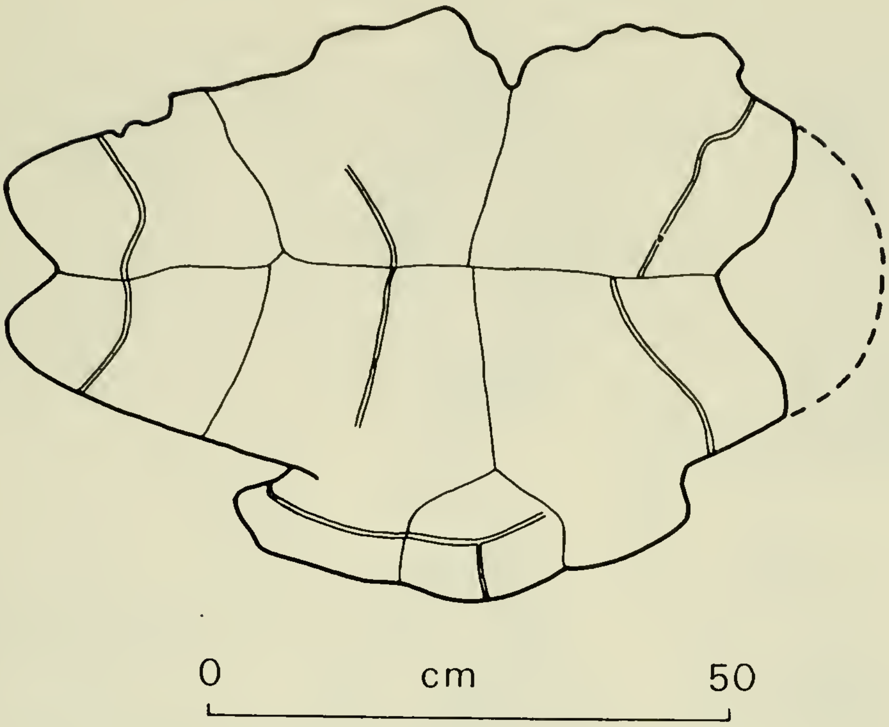

Figure 2. Sketch of a plastron (MCNC 245) referred to *Stupendemys geographicus,* showing the unusual position of the pectoral-abdominal scute sulcus. The full extent of the abdominal-femoral scute sulci cannot be traced.

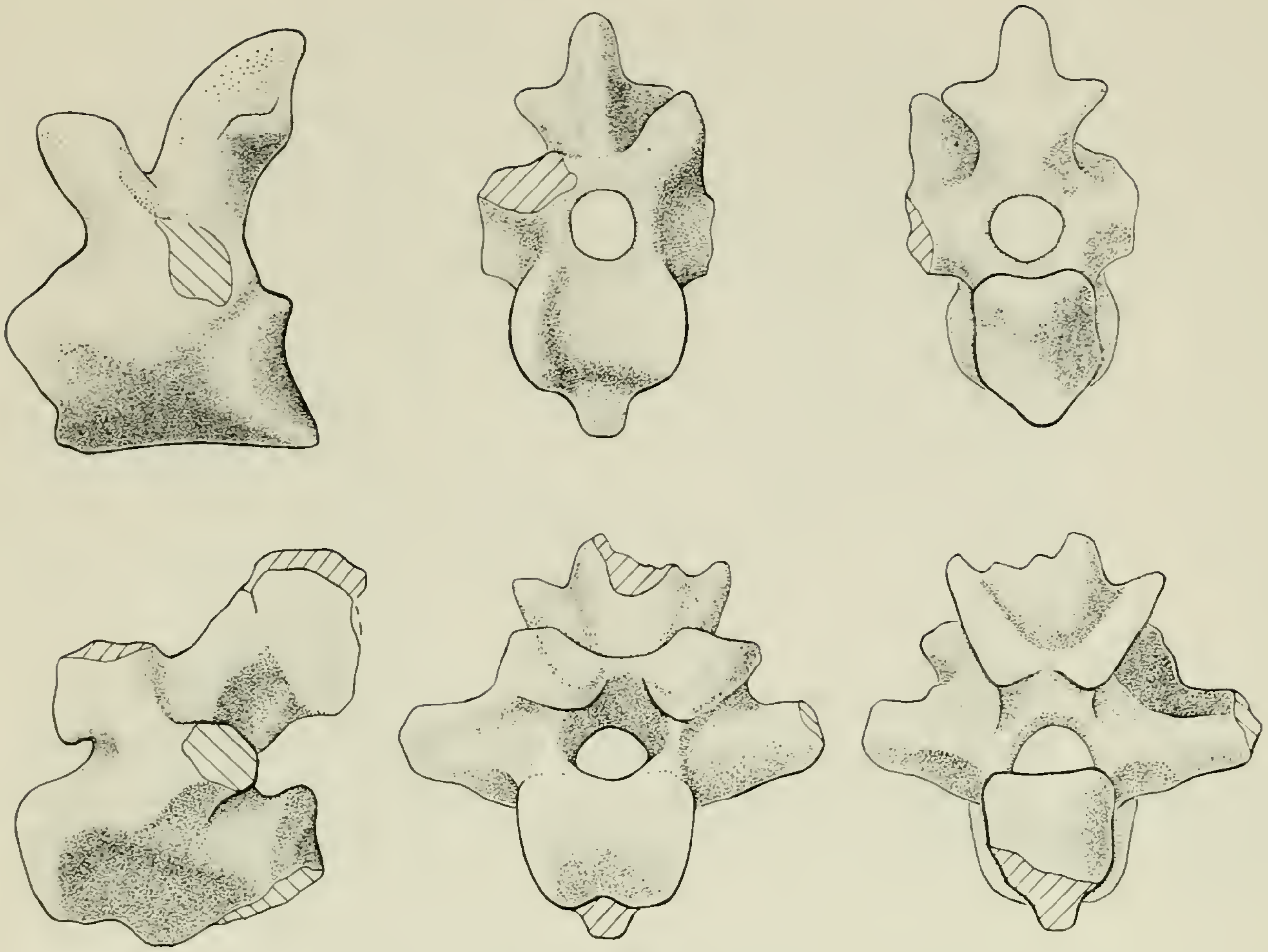

Figure 3. The seventh (bottom; MCZ[P]4376) and eighth (top; a composite based on MCNC 244 and MCZ[P]4377) cervical vertebrae of *Stupendemys geographicus* in left lateral (left), anterior (center), and posterior (right) views.

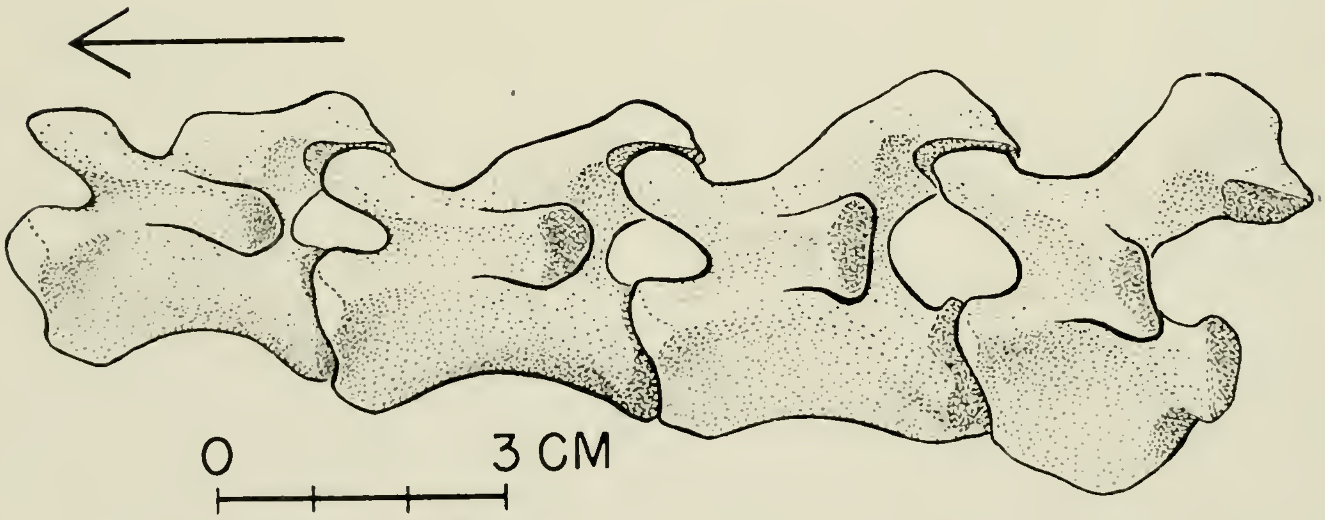

Figure 4. The fifth through eighth cervical vertebrae of *Podocnemis expansa* (MCZ[H]4469) in left lateral view. The arrow points toward the anterior end of the neck. Compare with the lateral views of Figure 3.

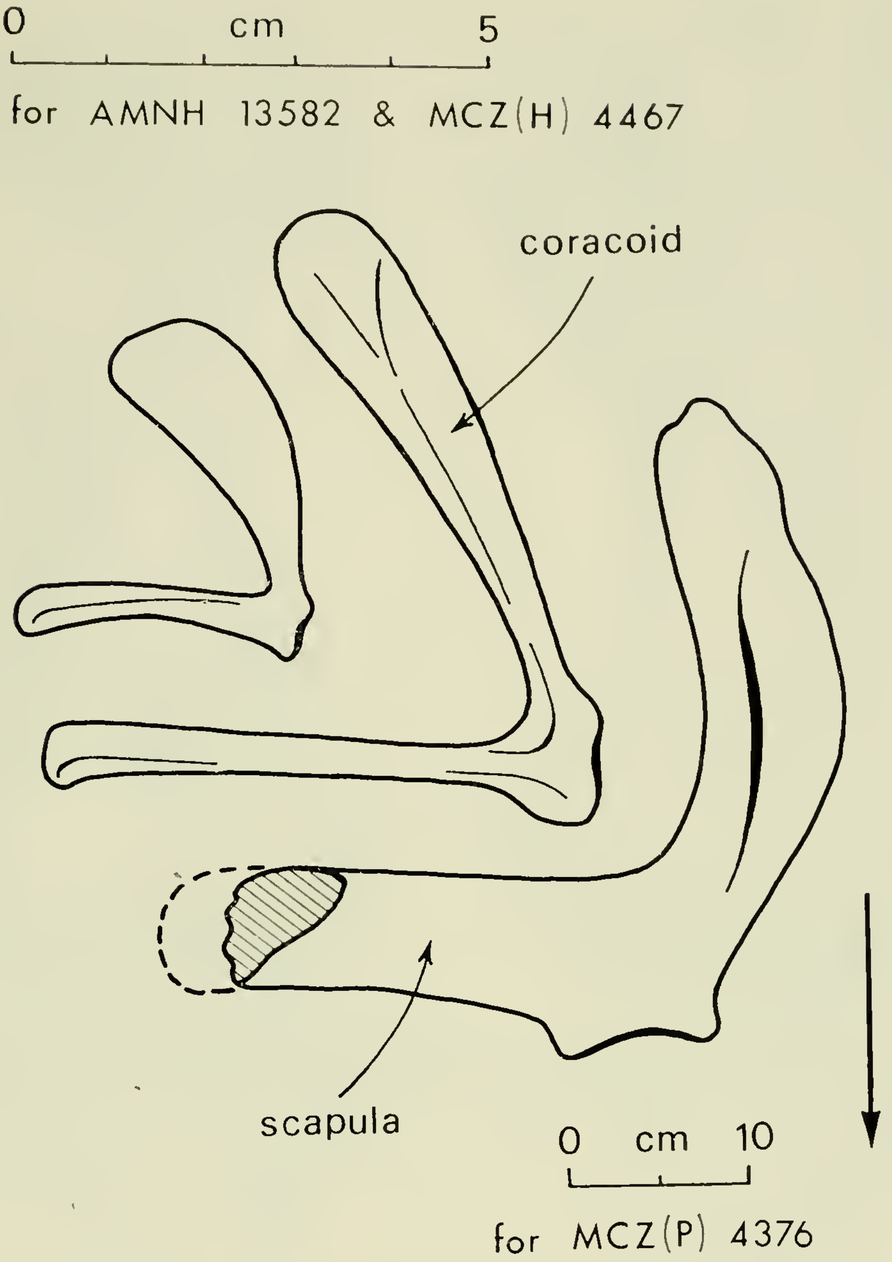

Figure 5. The ventral elements of the left scapulocoracoid of *Stupendemys geographicus* (MCZ[P]4376; bottom) juxtaposed with comparable bones of the Recent pelomedusids *Podocnemis unifilis* (MCZ[H]4467; middle) and *Pelusios castaneus* (AMNH 13582; top). The midline axis of the specimens to which they belong would be toward the left margin of the page. The arrow points anteriorly. The glenoid socket of the fossil faces forward while those of the Recent specimens are directed laterally. For clarity, the dorsal prong of the scapula and the suture between the scapula and coracoid have been omitted.

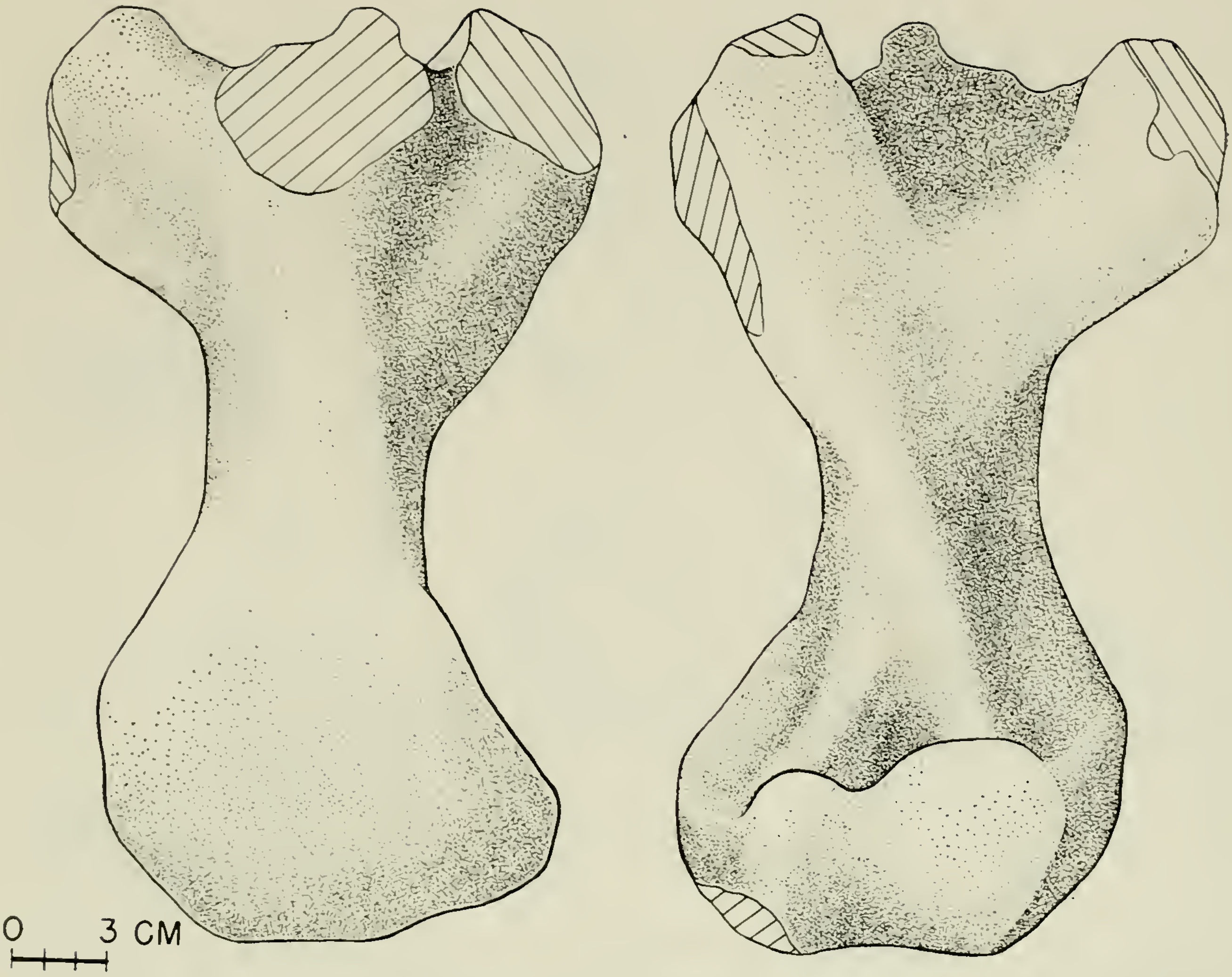

Figure 6. The left humerus of *Stupendemys geographicus* (MCZ[P]4378) in dorsal (left) and ventral (right) views.

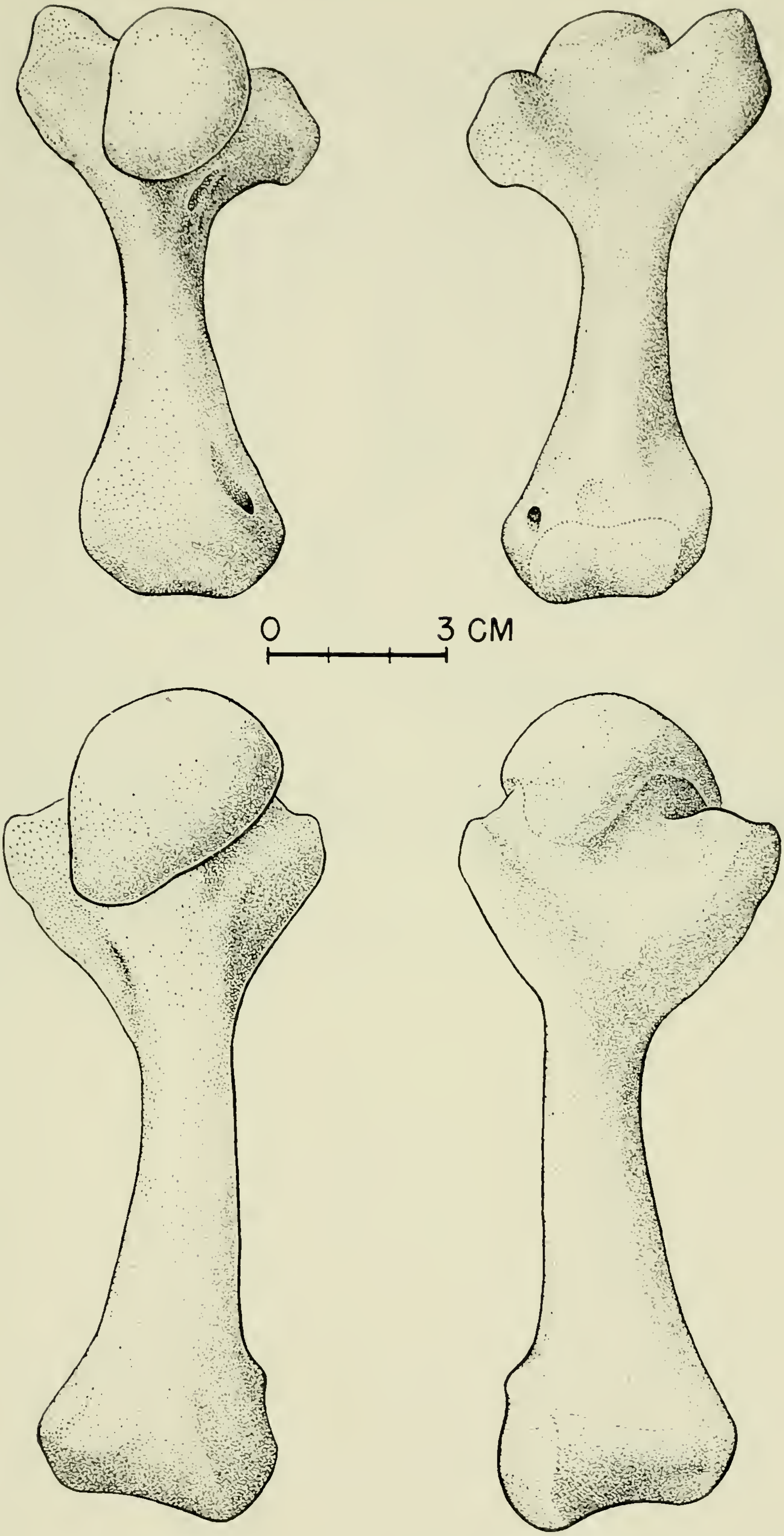

Figure 7. The left humerus (top) and left femur (bottom) of *Podocnemis expansa* (MCZ[H]4469) in dorsal (left) and ventral (right) views. Compare with Figures 6 and 9.

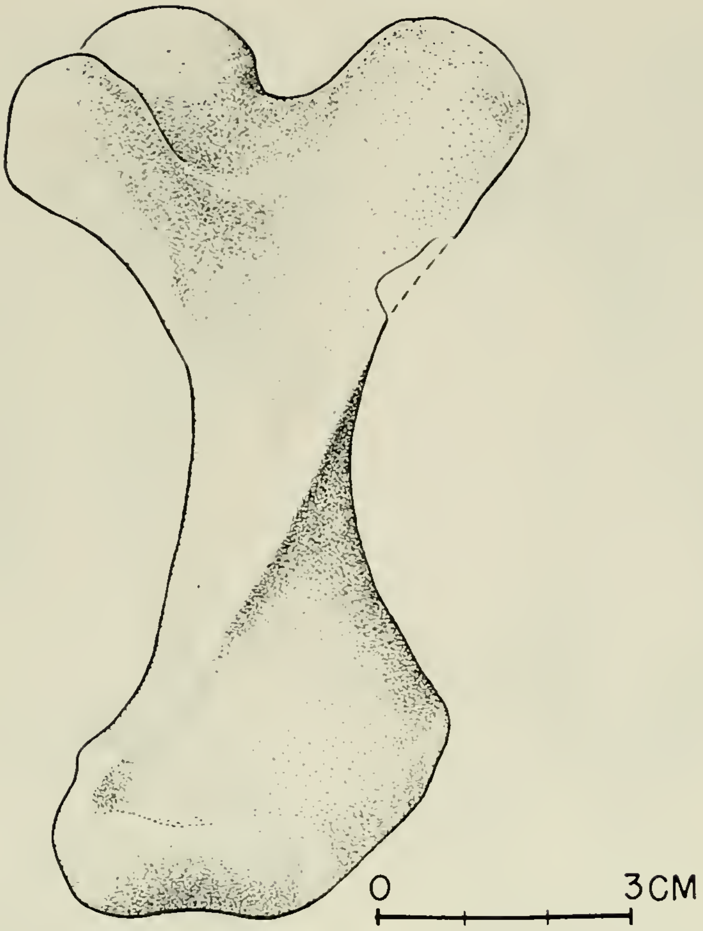

Figure 8. The right humerus of *Taphrosphys sulcatus* (PU 18707) in ventral view, showing the prominent ridge extending from the base of the ulnar process to just above the radial condyle. Compare with Figure 6.

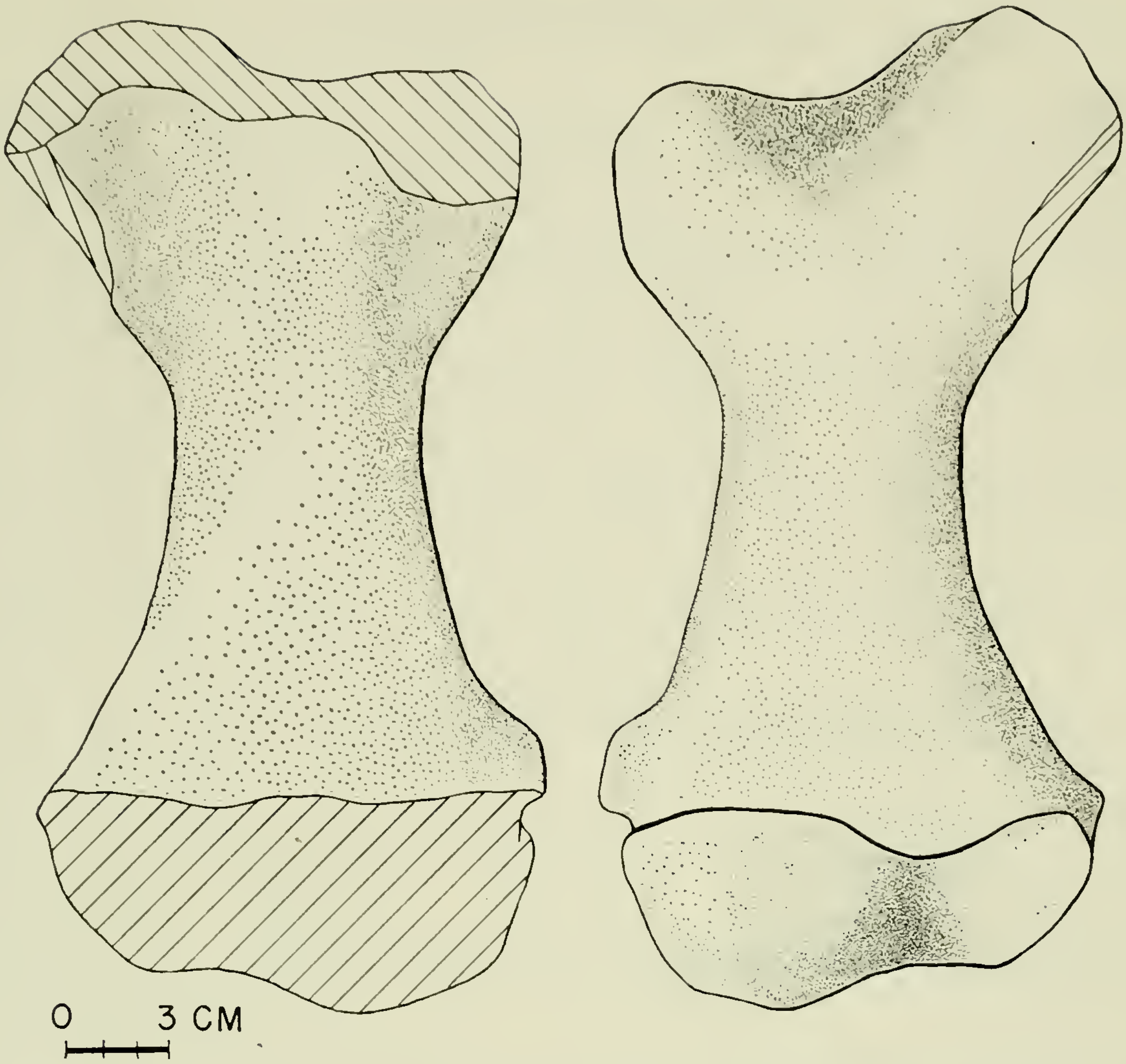

Figure 9. The left femur of *Stupendemys geographicus* (MCNC 244) in dorsal (left) and ventral (right) views.

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